PLANT FORMS

AND THEIR EVOLUTION IN SOUTH AFRICA

J. W. BEWS

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SOUTH WEST
AFRICAN
PROTECTORATE
GREAT NAMAQUALAND
BECHUANALAND
KALAHARI
SAND VELD REGION
BUSH VELD
TRANSVAAL
PORTUGUESE EAST AFRICA
Limpopo River
PRETORIA
Johannesburg
Vaal River
ORANGE FREE STATE
BLOEMFONTEIN
ASBESTOS HILLS
Orange River
RICHTERS VELD
Namaqualand
KAMIES BERG
VAN RHYNSDORP
KARROO
REGION
Sneeuw
Bergen
Storm Bergen
CAPE PROVINCE
Roggeveld Mts
Nieuwveld Mts
SOUTH WESTERN REGION
CAPE TOWN
Grahamstown
ADDO BUSH
Gr. Fish River
Port Elizabeth
BASUTOLAND
Orange R.
Griqualand East
NATAL
DRAKENSBERG Mts
Tugela R.
P.M.Burg
Durban
ZULULAND
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AND THEIR EVOLUTION IN SOUTH AFRICA

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*WITH MAP
AND ILLUSTRATIONS IN THE TEXT*

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To

BRIG.-GENERAL J. SCOTT WYLIE

PREFACE

The geographical distribution of plants is a subject that has always been full of interest, and it has been studied by many of the greatest botanists of the world. Of late years, in the light of modern knowledge, attention has been directed again to various aspects of it. It is being more and more clearly realised that plant geography has a bearing on many important problems, botanical and otherwise.

In the following pages an attempt is made to show that South Africa has much to contribute to our knowledge of this subject, and as many as possible of what appear to be the most interesting and important facts are put on record. The tracing of the probable evolutionary history of the vegetation of South Africa is a much more difficult task. It must be left to the reader to decide whether the facts recorded supply sufficient evidence to support the theories outlined.

The work as a whole may be taken to represent the view-point arrived at after fourteen years' study of South African vegetation. What future study and investigation may yield it is impossible to say. Some of the theories may require modification, but if the plant migrations into South Africa and the whole general ecological history of the vegetation have been as described, the bearing of it all on the study of the phylogeny of the Angiosperms is clearly full of great promise. At present the information gained in no way contradicts the more generally accepted principles of phylogenetic classification as applied to the flowering plants. At the same time many hitherto unnoticed details are brought to light.

The drawings were prepared by Miss Stella Gower, of the Union Division of Botany, and I have to thank her and the Chief of the Division, Dr. I. B. Pole Evans, who very kindly placed her services at my disposal.

J. W. Bews.

Natal University College,
Pietermaritzburg.
June 1924.

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INTRODUCTORY

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South Africa as a Field for Ecological Studies.—Of all the many varied aspects of modern botany, the ecological is in many ways most interesting, since it seeks to explain why plants are as they are, and why they occur in the places where they are found. In a sense all botany is ecological or has an ecological bearing, since, in so far as it is a science, it seeks to explain things. It has been said that plant ecology is not so much a branch of botany as a way of looking at the subject, and the more it advances beyond the stage of mere observation and classification, the more ecological botany becomes. Physiology and ecology are obviously closely allied, indeed much of the best ecological work so-called is simply physiological studies carried out in the field. The study of plant habitats leads on to the study of the general distribution of plants, and that has an intimate relationship to questions of evolutionary history. Darwin in one of his letters to Sir Joseph Hooker described the geographical distribution of plants as 'that grand subject, that almost keystone of the laws of creation.' Darwin's magnificent insight was not at fault. Since the publication of his 'Origin of Species' there has been an enormous accumulation of new discoveries in every branch of botany, many hypotheses have stimulated research in the effort to make clear the course of evolution, and we are now in a much more favourable

position for exploring the subject referred to by Darwin in such enthusiastic terms.

Few, if any, countries in the world are more favourably situated than South Africa for the study of plant distribution and its bearing on questions of evolutionary history. It is a country of widely diversified climates, from tropical to temperate, from very moist to very dry; it is an old country geologically; it has not suffered from the catastrophe of an Ice period; the history of its flora has been continuous since Permian times, and it is directly connected to the North with the great tropical reservoir of plant life. Its eastern and central and north-western regions of summer rainfall contrast strongly with the south-western region of winter rainfall and dry summers. Within comparatively small areas the topography influences the climate, and over the eastern side the hills and ridges and mountains which face the rain-bearing winds are clothed with subtropical forest or have subtropical grasses dominant, while the dry river-valleys have a highly specialised and derivative type of succulent and thorny scrub. The dry Karroo plains in the centre also possess a highly evolved type of flora. There is an opportunity, therefore, for endless comparisons, and if we can but read the story of its great plant migrations correctly we have a key to the history of the plants that are dominant over the whole world to-day—the Angiosperms.

South Africa undoubtedly presents great opportunities to the modern botanist. The problems are new, their solving turns the mind of the worker in new directions, and if the botanist reacts in the right way it is fairly easy to make progress. All botanists are probably influenced to a greater extent than other scientists by their environment, and the environment in South Africa is peculiarly stimulating. It has been remarked that if the science of botany had grown up in the southern hemisphere, it would be now a very different science. To a certain extent that statement is obviously true, though the science as a whole might not have advanced so far. Unless all the workers of the northern hemisphere could have been transported to the southern, progress would, of course, not have been so great. The development of laboratory technique and close association of morphology and physiology, or, in other words, the study of form and function together, has led to the steady development of the subject on sound lines. At the same time, if the great leaders of botanical thought (or some of them) during the last century had lived in South Africa, some aspects

of the subject would almost certainly have received more attention, including the study of plant distribution and plant growth forms. Of the latter, South Africa possesses such a great variety of types and so many of them are peculiar in their physiological aspects that they could hardly fail to receive attention.

Systematic botany, too, should not be allowed to grow all the time in the arid ground of the herbarium. Harvey's work in the first three volumes of the 'Flora Capensis' shows how much he gained by the years he spent in South Africa. The whole subject would probably have advanced more rapidly if the great systematists could more often have lived among the plants they were describing.

Some of the main characteristics of this land of botanical opportunity have been mentioned. Before proceeding to discuss the details of plant distribution and ecological evolution it has been thought well to consider the physical features, climate, and types of vegetation in a very general way. It is necessary to carry some such outline picture in mind while reading the chapters which follow. All unnecessary or less necessary details will be omitted from this account, and if more detailed information is desired regarding the first two items, it can be obtained from the articles of Rogers and Cox and Marloth in the 'Union Botanical Survey Guide.'

The Physical Features of South Africa.—South Africa consists of an elevated central plateau bounded by an escarpment from which the land descends more or less steeply to the sea. The whole land area is an old one, and only in Zululand and narrow strips along the coast have there been any additions to it in post-cretaceous times. Rogers estimates that over 40 per cent. of the present land area lies 4000 feet or more above sea level, and at the highest points of the eastern escarpment (the Drakensberg) altitudes of about 11,000 feet are reached. From the southern end of the Drakensberg range the escarpment bends across South Africa and is continued westward under the names of the Stormberg, Sneeuwberg, Nieuwveld, Komsberg, and Roggeveld. The river system of South Africa is very important in connection with its plant migrations, as will be explained more fully later. The greater rivers have formed pathways of migration for various trees and shrubs.

On the western side the escarpment is deeply cut into by the Orange river and its tributaries, though north of the Orange in the South-West Protectorate the escarpment is still a well-defined feature. The whole of the southern portion of the

great plateau is drained by the Orange and its main tributary, the Vaal. On the eastern side the various rivers run a shorter course and have cut down more steeply, leaving a system of high ridges in between. North of Carolina the escarpment ceases to be the watershed, the Limpopo having cut through it. Along the eastern river-valleys subtropical xerophytic scrub species of succulent and thorny trees and shrubs have migrated often far inland, and the same or allied species cross the continent along the Orange river and its tributaries.

The general steep grade of the rivers and the persistence of the escarpment are adduced by Rogers as evidence of geologically recent elevation in South Africa, though the elevation of the country was not accompanied by any considerable increase in area at the expense of the sea floor.

The physical features are, of course, to a large extent influenced by the climate. Along the coast there is a low-lying coast-belt. In the north-east it is covered by sand-veld, but from the middle point of Zululand southwards the sand is confined to a very narrow seashore strip. The actual coast-line has elevated fixed sand dunes covered with bush. The river-mouths of Natal have been ' drowned ' by a recent sinking of the land, and the mud lagoons formed as a consequence have a mangrove flora which extends as far south as the Komgha river mouth in the Cape. Rocky cliffs occur at only a few places and shingle beaches are very rare.

Behind the coast-belt on the eastern side the relatively high rainfall has produced deep valleys and ridges and hills fully clothed with vegetation, the valleys with xerophytic scrub and the rest with mesophytic grassland or forest, as already described. In the Cape there is a folded belt of mountainous country traversed by fairly wide or very narrow river-valleys between the Great Karroo and the coast. This is within the region, for the most part, of winter rains and dry summers, and the vegetation is dominated by heath-like and other shrubs of the Macchia. The Great Karroo itself is a dry region lying outside the escarpment, but its vegetation is essentially similar to the upper Karroo above the escarpment. The latter towards the east and north grades into grass-veld. In the whole of the dry areas of the centre and west the characteristic ' dryland ' type of scenery is found modified by the presence of harder doleritic or sandstone rocks through the Karroo shales. The flat plains have scattered xerophytic dwarf shrubs and succulents, the rocky hillsides somewhat taller shrubs, the whole flora having

close eastern and subtropical affinities. It is, however, highly modified as the result of the dry conditions.

North and west of the upper Karroo region lies the great sand-veld areas of the Kalahari and Bushmanland. This whole region is covered with sand which has drifted across it from the north-west. The central portion now consists of fixed dunes which run in a general direction from north-west to south-east. Towards the margin the sand cover is shallower, but though the rainfall is fairly high (from 10 to 20 inches, increasing from west to east) there is no surface water anywhere. The only mountains are those that surround it and low elevations of the ‘ inselberg ’ or island mountain type rising from it. It is a grass-veld country with scattered trees and scrub. West of the Kalahari and Bushmanland, the Namaqua Highlands, and north of the Orange river the mountains of the South-West Protectorate form the edge of the interior plateau. The Kamiesberg reach a height of 5510 feet and have a fairly high rainfall, but the Richtersveld is very dry. It is important to note that this dry belt is interposed south of the Orange river. There has been comparatively little migration along the western side of the continent southwards into the Karroo. The mountains north of the Orange river have an increasing rainfall northwards until grass-veld and bush are developed, but the flat western coastal plain, the Namib, is pure desert.

East of the Karroo and Kalahari is the great eastern grass-veld region, dominated completely by subtropical grasses showing increasing mesophytism from west to east. Most of it is treeless except along the water-courses, but in the Bushveld, a rather dry region with sandy soil, open tree-veld is developed. True mesophytic forest occurs on the eastern side, for the most part outside the escarpment. The Basuto Highlands include the highest portion of the Drakensberg (excepting the eastern face, which is in Natal). The flora at altitudes of 8000 feet and over is a mountain flora, connecting along the other mountain ranges of the southern escarpment with the south-western region of Macchia in spite of the fact that the latter has winter instead of summer rains.

The Climate of South Africa.—Various aspects of this subject have already been touched on, and the rest may be summarised rather briefly. The south-western region includes the portion of the sub-continent from Van Rynsdorp southward to the Cape and eastward to Humansdorp and Port Elizabeth, being bounded on the interior by the fold mountains which

limit the Karroo. There are, however, low-lying patches of the Karroo flora in the midst of it. The mean annual rainfall of this region varies exceedingly in different parts, from about 18 inches to 80 or more. Even in small areas the variation is great. In the Cape Peninsula some of the figures given over a period of thirty years or more are: Signal Hill, 18·63 inches; Platteklip (only a mile or two distant), 45·12 inches; Kasteel's Poort, 61·81 inches; St. Michael's (Table Mountain), 74·75 inches. Seventy-five per cent. of the rain in the south-western region falls in the winter season of low temperatures, but during the summer, while some parts remain dry, the effects of the hot weather are modified at higher altitudes by south-eastern mist-clouds, which supply the famous 'tablecloth' to Table Mountain.

Immediately to the east of this region there are transitional parts where the summer and winter rains are fairly evenly balanced, but all the rest of South Africa, as a whole, has summer rains and more or less completely dry winters, giving a well-marked resting-period to the vegetation, corresponding to that brought about by the lowering of temperatures in winter in the northern hemisphere. The amount of rainfall again varies greatly, and that within comparatively short distances. Thus in the Tugela valley in Natal the average annual rainfall is less than 25 inches, while on the forest-clad Qudeni heights above it a few miles distant, it rises to over 50 inches. Everywhere the valleys are dry, hot in summer and cold in winter, while the hills and ridges are moist and neither very hot nor ever very cold. The rain-bearing clouds come from the Indian Ocean and deposit moisture on the rising slopes until they have crossed the eastern escarpment. Westward from this the rainfall regularly decreases, the vegetation becomes more and more xerophytic till the process culminates in the Karroo and the desert regions of the west. The annual rainfall in the Karroo varies from about 14 inches on the eastern side down to less than 5 inches on the western. The desert regions of the west are said to have from one-half to an inch of rain annually on an average of a period of years, but several years may pass without any rain at all, and at any rate the figures are not very reliable.

The temperatures of the various parts of South Africa, as a whole, are much affected by the altitude of the central plateau, so that there is in a general way a considerable degree of uniformity over the whole sub-continent. The cold Benguela

current on the western side and the warm Mozambique current on the east lead to a bending southwards of the isotherm lines on the eastern side, or, in other words, stations of the same latitude are warmer on the eastern side than on the western. The eastern coast-belt is free from frosts in winter, a fact of importance in connection with the tropical origin of the South African vegetation, since purely tropical species like the Mangroves and many other coast-belt types are able to penetrate far south on this side and the modified and derivative subtropical flora of the central areas have had chiefly an eastern origin.

Just as topography influences the rainfall even in small areas, so it has a marked effect on temperatures and on the total amount of insolation. It has already been stated that the valleys are not only very dry but they are very hot. This is due largely to the effects of radiation from the two sides. The side of the valley which faces the north and receives the full effect of the sun throughout the day has a much more xerophytic plant covering than the opposite side. During the winter anticyclonic conditions, cold-air drainage down the valleys lowers the temperature regularly in many parts below freezing-point, though the higher slopes may remain free from frosts. The influence of aspect and slope exposure is also seen on the hills and kopjes. The northern slope facing the sun has a more xerophytic but often more tropical type of vegetation than the slope facing south. The total amount of insolation is much greater on the northern side. We have measured and compared differences from time to time instrumentally, but it can also be worked out mathematically since the angle of the sun's rays is known at each latitude throughout the year. Roughly a slope with an angle of 30 degrees to the horizontal has an increased amount of insolation equivalent to a shift of 15 degrees of latitude northward. Observations made on Signal Hill near Maritzburg throughout a whole day in winter showed that the north slope with a moderately steep gradient (30° with horizontal) received a total amount of light sufficient to liberate 146·5 milligrams of iodine from a solution of potassium iodide and sulphuric acid, while the south slope (45°) received an amount in the same time sufficient to liberate only 104·3 milligrams from an equivalent solution. In summer the corresponding figures for a day were 235·2 on the north slope and 218·2 on the south. It is not surprising, therefore, to find so many tropical and xerophytic species of trees

and shrubs on the northern slopes of the Transvaal kopjes while the southern slopes have more typical South African vegetation.

It is not surprising, also, to find the south sides of the river-valleys of Natal which face north covered with Euphorbias, Aloes, and thorn trees, while the opposite sides facing south have smooth grassy slopes with mesophytic scrub and forest developing as a climax on the higher flanks.

Light intensities in South Africa are uniformly high (see Bews and Aitken, 1923), and a regular increase is shown with rise in altitude. Johannesburg receives as much actinic light in one day as Manchester receives in a month of winter weather, but the longer daylight in summer of higher latitudes compensates to a certain extent. In the great mass of associated (geophytic) grass-veld plants of South Africa assimilation takes place very rapidly during early spring. Our measurements of light intensities have shown the remarkable clearing effect on the atmosphere of the frequent summer rains over eastern South Africa—a fact already familiar to photographers.

The general movements of the air are of importance chiefly in connection with the rainfall, but apart from the rain-bearing or mist-forming winds, the Foehn winds are important. These are hot winds which blow regularly down the valleys of the eastern side at intervals during the spring and early summer. They have an extreme parching effect on the vegetation. It is surprising, however, how quickly most plants are able to restore their water balance, as well as to resist reducing it below the fatal minimum. Few plants are ever killed by the hot winds, though the newcomer to South Africa usually compares them to the experience of standing much too near the open door of a very hot oven.

They are generally followed immediately by heavy rains which restore at once the turgor of the plants and the good temper of the inhabitants. The strong hot winds raise great clouds of dust, since they occur after months of dry weather. The rains wash down all the dust and leave the air for a few days remarkably pure. Growth takes place with wonderful rapidity. The numerous bulbous and tuberous plants which have lain buried in the soil during winter shoot up and flower and the whole grass-veld of large areas is transformed into a magnificent flower garden. The trees and shrubs of the scrub and forest areas also flower as a rule in the early spring.

The Two Floral Elements and Main Types of Vegetation in South Africa.—A general sketch of the vegetation of South

Africa, different aspects of which will be dealt with in detail in later chapters, may not be considered out of place at the present stage. Some such outline picture again is necessary for the full understanding of what follows.

There are two main floral elements in South Africa: the one tropical-subtropical covering the eastern, central and north-western regions, and the other a temperate element confined to the south-west and the central and eastern mountain ranges. There is, of course, a certain amount of mixing of the two elements. Numbers of tropical-subtropical species occur in the south-west even as far as the Cape Peninsula; a few temperate genera have produced species that hold their own even right down to the coast of Natal, and on the eastern mountains the mixing of the two elements is considerable. The two elements not only differ ecologically but are almost certainly different in origin, yet among subordinate types of growth form and associated non-dominant plants (*e.g.* the bulbous Monocotyledons) there are many large genera well represented in both.

The tropical-subtropical vegetation of South Africa shows a great range of ecological differentiation. Tropical tree growth is seen in the Mangrove flora of the river mouths, in the Barringtonia association of wet sandy soils on the coast and in the hygrophilous forest of the eastern side, which occupies stream-banks and swamps in the frost-free localities. The mesophytic eastern high forest, with *Podocarpus*, etc., dominant, is more subtropical, though in the main the tropical growth-form characters are retained. The forests occupy the rising slopes which face the rain-bearing clouds from the Indian Ocean, and they are surrounded by a belt of mesophytic scrub dominated by light-demanding, not very tall trees and shrubs. The genus *Rhus* and numerous Rubiaceae, *Rhamnus prinoides*, *Buddleia* spp., etc., are prominent in this type of scrub which often occurs in forest areas where high forest has been destroyed or has not developed.

In somewhat drier areas trees have invaded the grass-veld and grow sometimes isolated with wide open spaces between the individuals, or as the plant succession advances the various pioneers become the centre of clumps containing a large variety of slightly more mesophytic species of trees and shrubs with undergrowth. The general name 'Tree Veld' may be applied to this parkland type of tree growth in South Africa. Many varieties of it occur. The Bush Veld of the Transvaal has *Terminalia*, *Combretum*, and various Leguminous trees dominant

associated with numerous others. Further north and extending into the tropics *Brachystegia* Veld covers vast stretches, while *Copaifera mopane* and *Adansonia digitata* form areas of Mopane and Baobab Veld. In the river valleys of the eastern side and over stretches of the interior and west *Acacia* spp. are dominant over great areas of 'Thorn Veld.' *Hyphaene crinita* forms 'Palm Veld' in sandy areas of the Natal coast-belt and Zululand, and *Hyphaene ventricosa* occurs similarly on the western side.

The south-western flora has even succeeded in invading eastern grass-veld and forms the Protea Veld of the foothills of the Drakensberg, but *Protea* spp. occur also in *Brachystegia* Veld. The most highly modified and specialised of the sub-tropical trees and shrubs are seen in the growth forms which are dominant in the succulent and thorny scrub of the eastern river-valleys. It sometimes represents the climax of xero-phytic thorn-veld, but though thorn trees (Acacias) occur in it, they are not so prominent as the tree Euphorbias, Aloes, Gymnosporias, *Portulacaria afra*, etc. This type reaches its fullest development in the Fish river areas bordering the eastern Karroo.

Many subordinate types of growth form, such as climbers, epiphytes, undershrubs and forest herbs, are associated with the trees and shrubs.

The second great class of growth forms of tropical origin in South Africa are those which compose the various grasslands that cover practically the whole of the summer rainfall area except the Karroo and desert regions of the west. Such parts as are invaded by tree growth are not so extensive geographically.

There is considerable variation in water content throughout this type. The marsh or vlei areas are dominated by Cyper-aceae and marsh grasses. The true aquatics are a subordinate and derivative type. The dominant grasses belong mostly to the tribes Andropogoneae and Paniceae. The Red grass, or Rooigras (*Themeda*), is dominant over wide areas, and there are numerous species of *Andropogon*. The taller grasses (*Cymbo-pogon* spp. and others) are hygrophilous vlei margin or forest margin transitional types in the succession. Some pioneer or psammophilous grasses are surface-rooting creepers, but the majority are tufted bunch grasses which, towards the drier parts of the interior bordering the Karroo and on the west side, consist largely of *Aristida* and *Eragrostis* species.

These are dominant genera also in the early stages of the

plant succession over all the grassland areas, though they are derivative types. Always as the succession advances towards the mesophytic it tends to become more and more tropical. This applies also to succession in scrub and forest. The relatively more xerophytic, derivative subtropical types prepare the way and allow of a southward extension of the relatively unmodified mesophytic more tropical types.

With the establishment of grassland areas, a vast assemblage of subordinate associated types has been produced. Plants with various types of underground storage (geophytes), rhizomes, tubers, bulbs, are most prominent. These draw upon their accumulated stores of water and food and develop and flower in the spring, forming ‘vernal aspect societies.’ Dwarf shrubs and suffrutices tend to compete more directly with the grasses and are often transitional in the succession to scrub and forest.

In the Karroid central region the grasses play a subordinate part. The dominant vegetation consists of dwarf shrubs and succulents associated again with geophytes, annual plants and scattered xerophytic grasses. The Compositae (*Pentzia* spp., etc.) are particularly prominent in all the large transitional areas. With increase of aridity the annuals become still more prominent ; only the most xerophytic dwarf shrubs and succulents remain, and these in the desert areas of the west grow far apart, leaving great sandy or stony stretches entirely bare. In the Karroo and desert areas *Pentzia*, *Lycium*, *Rhigozum*, *Crassula*, *Mesembrianthemum*, *Sarcocaulon*, *Euphorbia*, *Stapelia*, *Hoodia*, *Senecio*, (*Kleinia*), and *Salsola* are some of the prominent genera. The whole of this extremely xerophytic flora represents the final result of specialisation in South Africa of the subtropical flora in response to arid conditions.

The Temperate or Mountain and South-Western vegetation of South Africa is more homogeneous. It is completely dominant in the region of winter rains in the south-west, where it contains a large number of genera and species including a high proportion of endemics. It extends along the central and eastern mountains and with interruptions through the mountains of the tropics to Abyssinia, and connects even with the European vegetation of the Mediterranean. To speak of it as a ‘Mediterranean flora,’ however, is misleading, though it is of a similar ecological type. The South African term Fynbosch should be maintained for it as equivalent more or less to the term Macchia. It consists of hard-leaved, often heath-like,

small trees and shrubs. The majority of the component species are woody, though they may be much dwarfed. The Proteaceae, Ericaceae, Compositae, Restionaceae, Bruniaceae, Penaeaceae, Rutaceae, Geraniaceae (*Pelargonium*), Verbenaceae, and the bulbous Monocotyledons with various Gramineae (*Danthonia*, *Pentaschistis*, etc.) as associated plants are most prominent in it, but it will be analysed in detail in a subsequent chapter.

CHAPTER II

PLANT FORMS AND THEIR EVOLUTION

The classification of growth forms or life forms—Ecological evolution—Primitive unchanging types of habitat—The influence of increasing aridity—Non-persistent types of habitat—Evidence from phylogeny—An outline of the evolution of growth forms.

The Classification of Growth Forms or Life Forms.—Warming (1909) used the term ' growth form ' for the concept which he defines as follows :

' Just as species are the units in systematic botany, so are growth-forms the units in ecological botany. Every species must be in harmony, as regards both its external and internal construction with the natural conditions under which it lives; and when these undergo a change to which it cannot adapt itself, it will be expelled by other species or exterminated. Consequently one of the most weighty matters of œcological plant-geography is to gain an understanding of the epharmony of species. This may be termed its *growth form* in contradistinction to its *systematic form*. It reveals itself especially in the habit and in the form and duration of the nutritive organs (in the structure of the foliage-leaf and of the whole vegetative shoot, in the duration of life of the individual and so forth), but shows to a less extent in the reproductive organs. This subject leads us into deep morphological, anatomical, and physiological investigations ; it is very difficult yet very alluring ; but only in a few cases can its problems be satisfactorily solved at the present time. Thus we impinge upon the problem of the origin of different species.'

Under the influence of Warming, the term ' growth form ' has become widely used in English and American botanical teaching and is here retained, but, as Clements (1920) rightly points out, the terms ' vegetation form ' used by Humboldt (1805) and Grisebach (1872), and ' life-form ' used by Drude (1890, 1913), Raunkiaer (1905), Clements (1920), ' have the preference both by priority and significance.'

Summaries and criticisms of the different systems proposed by various authors of classifying plant ‘ life forms ’ or ‘ growth forms ’ are given by Warming (1909), by Clements (1920) and others. With the exception (to a certain degree only) of that of Raunkiaer they have much in common, being founded, as Clements points out, more or less on the two principles enunciated by Drude—namely, (1) the rôle played by a particular species in vegetation and (2) its life history under the conditions prevailing in its habitat, with special reference to duration, protection, and propagation.

Raunkiaer's system (1905) is based primarily on the degree of protection to the buds during the winter resting season. The main classes are: *Phanerophytes*, or trees and shrubs (subdivided according to size and whether evergreen or deciduous); *Chamaephytes*, with buds near the surface of the ground, protected by snow or fallen leaves (suffrutescent, passive and active chamaephytes and cushion plants); *Hemicryptophytes*, with buds at soil level (rosette plants, subrosette plants, etc., with or without creeping offshoots); *Geophytes*, with underground storage organs (rhizomes, tubers, bulbs); *Helophytes* (marsh plants); *Hydrophytes* (water plants); and *Therophytes* (annual plants).

Raunkiaer's system is fairly easy to use, and I have applied it in a former paper to the vegetation of Natal (Bews, 1916). While Raunkiaer's system by being based on one single viewpoint is remarkably consistent, it fails to meet the requirements of ecology as a whole, or to define growth forms as the units of ecological botany in the same way as species are defined as the units of systematic botany. One of Raunkiaer's most important contributions has been the application of statistical methods in determining the climatic relations of any particular flora. His ‘ normal spectrum ’ is an estimated percentage representative of each class of growth form in the whole world's flora. By comparing the percentages in any local flora, the salient features of the climatic correlations are brought to light. Thus a high proportion of Phanerophytes shows a climate of sufficiently high rainfall, etc., to favour forest development. Chamaephytes are relatively abundant in regions where there is a winter covering of snow. Therophytes are a test of desert conditions or of regions of high cultivation, etc. The important thing is the degree of difference in the percentages from the ‘ normal spectrum.’

In Natal it was found that the Phanerophytes, as a whole,

fell considerably below the normal—31 per cent. instead of 43 per cent.; but though it has less than more tropical regions, it has far more trees and shrubs than countries in the northern hemisphere—*e.g.* Denmark, which has only 7 per cent. The percentage of Geophytes in Natal is very high, 18 per cent., as compared with 3 per cent. in the whole world's flora. This type is peculiarly suited to South African grass-veld conditions. The Hydrophytes and Helophytes are grouped together by Raunkiaer, who gives only 1 per cent. of both for the whole world's flora, a percentage that appears much too low. At any rate, Natal has nearly 6 per cent. Therophytes in Natal are about 6 or 7 per cent., only half the normal, but figures for the western side of South Africa would show a much higher percentage. Natal is far removed from desert conditions and it is not under high cultivation.

The classification of plant life forms owes much to Drude, who has modified his earlier systems until, in his latest (1913), he makes three main divisions: *Aerophytes*, *Water plants*, and *Mosses and Thallophytes*. These he divides into 55 types and several subtypes. Pound and Clements in their work on the vegetation of Nebraska (1898) modified the earlier system of Drude to suit American conditions, but in his later work (1920) Clements states that much the most useful and consistent view of life forms is obtained from a single point of view—that of vegetation. 'The development and structure of vegetation are chiefly a matter of dominants and subdominants and it is the life forms shown by these which are of paramount importance. Hence it becomes desirable to speak of them as vegetation-forms as Drude did originally, following Grisebach and Humboldt.'

The major divisions given for Vegetation Forms are: (1) Annuals, (2) Biennials: Herbaceous perennials, (3) Sod grasses, (4) Bunch grasses, (5) Bush herbs, (6) Cushion herbs, (7) Mat herbs, (8) Rosette herbs, (9) Carpet herbs, (10) Succulents: Woody perennials, (11) Half shrubs, (12) Bushes, (13) Succulents, (14) Shrubs, (15) Trees.

Warming (1909) prefaces his system of classifying growth forms by saying: 'It cannot be sufficiently insisted that the greatest advance, not only in biology in its wider sense but also in œcological phyto-geography, will be the œcological interpretation of the various growth-forms: from this ultimate goal we are yet far distant.' He states further that it is difficult to discover guiding principles that are really natural.

'Genetic relationships, and purely morphological or anatomical characters, such as the venation and shapes of leaves, the order of succession of shoots, monopodial and sympodial branching, are of very slight œcological or of no physiognomic significance. Œcological and physiological features, particularly the adaptation of the nutritive organs in form, structure and biology to climate and substratum or medium, are of paramount importance. Cases, however, are not wanting in which œcological grouping runs parallel with systematic classification.'

Warming then divides growth forms into six main classes: (1) Heterotrophic, (2) Aquatic, (3) Muscoid, (4) Lichenoid, (5) Lianoid, (6) All other autonomous land plants. It should be noted here that unlike many of the other authors mentioned, he maintains the Lianes as a main class. He divides his large sixth class into: (I.) Monocarpic herbs and (II.) Polycarpic plants. In the subdivision of the latter he lays stress on (1) the duration of the vegetative shoot, (2) length and direction of the internodes, (3) position of the renewal buds, (4) structure of buds, (5) size of the plant, (6) duration of the leaves, (7) the adaptation of the assimilatory shoot to the conditions of transpiration, (8) the capacity for social life; and in accordance with these considerations he divides Polycarpic plants into (*a*) Renascent herbs, (*b*) Rosette plants, (*c*) Creeping plants, (*d*) Plants with erect long-lived shoots. Each of these subclasses is then further subdivided.

As already stated, all the systems have much in common, and it is clear that growth-form classification has gradually been reaching towards a stage corresponding to that arrived at by systematic botany when the known plants had been classified into alliances, cohorts or orders, and these into families, tribes and subtribes, etc. The arranging of the groups in a sequence following evolutionary history is still almost as difficult a matter in systematic as it is in ecological botany. A linear sequence is clearly impossible. The construction of 'phylogenetic trees' is only partly possible, since the main trunk and branches have disappeared in the process of plant differentiation and we only possess at the present day the ends of the branches.

Fossil botany supplies information that helps but only very slowly. Every branch of botany assists. The anatomical studies of many distinguished botanists have thrown a great deal of light on the origin of various plant forms. Under the influence of Haberlandt and others, the study of physio-

logical anatomy is gradually supplying firmer foundations on which to build.

Darwin, as we have seen, believed that geographical distribution is the 'keystone of the laws of creation,' and it is the object of the present work to try to show, however inadequately, that he was probably, to a large extent, right.

Apart from the life forms, ecologists have classified plants according to their ecological distribution into what Clements calls 'Habitat forms.' Warming (1896) first divided them into Hydrophytes, Mesophytes, Halophytes, and Xerophytes. Later (1909) he expanded his classification into the following classes: (1) Hydrophytes (water plants); (2) Helophytes (marsh plants); (3) Oxylophytes (plants of sour soils); (4) Psychrophytes (plants of cold soils); (5) Halophytes (plants of saline soils); (6) Lithophytes (rock plants); (7) Psammophytes (sand plants); (8) Chersophytes (plants of waste land); (9) Eremophytes (desert and steppe plants); (10) Psilophytes (grassland plants); (11) Sclerophyllous plants (hard-leaved); (12) Coniferous formations; (13) Mesophytes. Other classes recognised by various writers include Heliophytes (sun plants) and Sciophytes (shade plants) and (by Clements) Drymophytes (bushes, shrubs, and small trees).

Ecological Evolution.—Hitherto ecologists have not attempted to arrange the various life-form classes in any evolutionary series, though it is clear that if they have been produced by a gradual process of 'epharmosis,' if in general they reflect the changes of environment which they have undergone in the past, and if the past changes of climate were known, it should be possible to arrange them in some sort of natural sequence. A beginning has been made by Jeffrey, Eames, Sinnott and Bailey, and others who believe and have brought forward much evidence from anatomy, morphology, phylogeny and geographical distribution to prove that the woody type of flowering plant is in general more ancient than the herbaceous. The aquatic type among Angiosperms is generally looked on as derivative, as are subordinate types of growth form, such as parasites, epiphytes, etc. But botanists generally have devoted attention to the reproductive processes in seeking to determine affinities. Now among the Angiosperms evolution in flower structure has been correlated with a very different environment from that influencing vegetative form. Evolution in the insect world has had an important effect on flower structure, but evolutionary changes in the latter, it

may be argued, have often been entirely independent of the environment.

For purely aquatic plants the environment cannot have changed very much; yet, as Willis (1915) has pointed out, such a group as the Podostemaceae have large numbers of genera and species, and aquatics generally have undergone considerable evolutionary change.

In the same way, tropical forest, while remaining uniform and stable in its climate, has produced an overwhelming variety of genera and species and is not dominated by a few, as might reasonably have been expected. Physiological stability would seem to be associated with germinal instability. New species arise most frequently among types adapted to a narrow range of environmental factors, whereas plastic types capable of growing under a wide range of conditions are relatively few in number and remain few.

While evolution in flower structure and reproductive process has not run altogether parallel with evolution in growth forms, yet there is, as will be shown later, a certain amount of interrelationship between the two, and if botanists were agreed about the general course of evolutionary history in the former, it would assist us greatly in the attempt to classify the latter on evolutionary lines. Unfortunately this is not the case. Among the systematists there are at least two distinct, or indeed almost opposite, points of view.

The one regards simplicity, the other relative complexity of structure in the flower as primitive. On the one hand, plants with achlamydeous or monochlamydeous flowers, few stamens, and a single ovary, are looked upon as the most ancient unspecialised types. Of recent systems of classifying flowering plants, Engler's follows this as a general guiding rule. The Pandanaceae, the Helobieae, and the Glumiflorae among the Monocotyledons, the Verticillatae (*Casuarina*), the Piperales, the Juglandales, the Fagales, the Salicales, etc., among the Dicotyledons, are placed at the beginning of the scheme of classification as being presumably the most primitive. Complexity of flower structure is considered to follow on increased adaptation to insect visits and to show advance. *Casuarina* shows certain possible connections with *Ephedra* among the Gnetales (see Macfarlane, 1918).

On the other hand, a considerable number of systematists, while admitting the general increasing adaptation to insect visits and consequent increasing complexity of floral envelopes

and various pollination mechanisms, hold the view that general simplicity of structure in the essential organs of the flower, especially the presence of a single ovary with few to one ovules and few stamens, is usually the mark of high evolutionary advance. They lay stress on the idea that economy combined with efficiency has been one of the guiding principles to success in the plant world, as it is in human affairs. They regard the Ranales, where this is least achieved, as probably the most ancient forms of Angiosperms and would connect them with the Bennettitales among fossil Gymnosperms. It is, of course, quite possible that both views are partly right. It is reasonable to suppose that simplicity of structure is sometimes primitive, sometimes arrived at after a long evolutionary struggle. Nor is there any reason why the Angiosperms should not be diphyletic or even polyphyletic in origin.

While the Monocotyledons are usually placed before the Dicotyledons in the older systems of classification, there has been a tendency in modern times to regard the former as derivative from the latter. The exact mode of origin of the Monocotyledons has led to the rival theories of syncotyly (or fusion of two cotyledons to form one) and heterocotyly (where there is division of labour between the cotyledons and one becomes suppressed). Bancroft (1914) has given a full review of the literature on the subject. Henslow (1893, 1911) looks upon the Monocotyledons as derived from Dicotyledons 'through self-adaptation to a moist or aquatic habit.' Miss Sargent (1903) put forward a theory of the origin of Monocotyledons founded on the structure of their seedlings favouring the view of syncotyly and laying stress on the tendency towards a geophilous habit.

Very recently (1923) Hoskins has published a paper describing what he takes to be a monocotyledonous stem, *Angiospermophyton americanum*, from the Carboniferous of Illinois. He states that while this discovery throws no light on the phylogenetic origin of Angiosperms, it does remove the problem from the Mesozoic to the Carboniferous or pre-Carboniferous.

The section of Clements' work on 'Plant Succession' (1916) dealing with past climates and climaxes, forms the most complete attempt to investigate the geological history of flowering plants. The tables of genera there included by courtesy of Dr. F. H. Knowlton afford a very complete summary of the fossil evidence. Chamberlin and Salisbury (1906) also give the conclusions that appear justifiable from the geological

evidence regarding climatic and other changes in the past. It is important to know that the geological evidence is not dependent entirely on the fossil record. Salt beds, Gypsum beds, and Red beds are all good evidence of arid conditions. The signs of glaciation are also important with regard to past climates. Since the rise of the Angiosperms there have been many climatic changes, great alternating cycles of favourable and unfavourable conditions, which naturally involved changes in the vegetation and altered the course of evolution. Such cyclic changes, however, would not involve the whole world's flora simultaneously and to the same extent.

Primitive Unchanging Types of Habitat.—There are certain plant habitats which existed and were widespread and uniform at the time of the rise to dominance of the Angiosperms. These have remained relatively constant and uniform ever since, and it is reasonable to suppose that primitive types of growth form are most likely to occur in such habitats.

1. The first and most important of these are the moist, warm, tropical forest habitats. Such conditions were more widespread in Cretaceous times than they are now. Tropical fossil species are found over a very wide range of latitudes. Though their boundaries may have contracted and expanded many times, it is reasonable to suppose that the hygrophilous megatherm formations of the world to-day are among the most ancient ecological types. It is interesting to note that Engler (1905) finds connections between these formations in Western tropical Africa and tropical America, while tropical Africa connects still more closely with India and Madagascar. The dominant growth forms are trees with large undivided leaves, but lianes and derivative undergrowth are more highly differentiated.

2. Stream-banks and swamps. Here excess of water is the dominating factor, and water does not change its essential character and influence on the vegetation. In any particular locality this habitat is highly unstable, but though it changes its position, it does not, as a rule, disappear entirely and, as long as it remains, its vegetation is relatively unaffected by climatic changes. Marsh and water plants and hygrophilous stream-bank species also migrate readily and easily, and tend to have a very wide distribution. Aquatic and marsh plant communities over great areas in any country are exceptionally uniform even when the climatic factors vary greatly, a fact which is particularly true of South

Africa. Thus, over the whole eastern side there is remarkable uniformity of composition in vlei vegetation from the coast to the Drakensberg through different climatic areas. Probably also with great climatic changes in the past, aquatic and marsh vegetation remained relatively unchanged, though new species invaded the habitat from time to time as they were produced in the course of evolutionary history.

3. Seashore habitats. The dominating factors in this case are the presence of salt or brackish water, mud or sand, and the climatic influence of the neighbouring sea. As in the case of marsh and aquatic habitats, migration along the seashore is at the present time, and probably always has been, relatively an easy matter. Though many obviously recent and derivative growth forms are found along the seashore, at the same time it is the habitat of some probably very ancient types, e.g. *Casuarina*, *Leitneria*, *Batis*, *Pandanus*, various Helobieae, the Mangroves, etc.

4. It is a little doubtful whether mountain habitats should be added to this list. As in the case of aquatic and streambank habitats, these are highly unstable, yet they preserve their essential characters, and mountain species at the present time are often widespread. Many admittedly ancient types are mountain species, and, as we shall see later, the mountain flora of Africa is in many respects an old one.

The Influence of Increasing Aridity. Non-persistent and Derivative Types of Habitat.—While the main types of plant-growth form, both woody and herbaceous, were evolved long before the rise of the Angiosperms, at the same time modern Angiosperms do show without doubt a much greater general diversity of form than the plants of earlier geological epochs. Aridity has been the chief factor in bringing about this extensive differentiation. Extensive periods of desiccation are indicated by the geological facts in palaeozoic times, and Calamites, Lycopods and other fossil groups have been described as xerophytes, yet, as Macdougall (1909) has pointed out, ‘ their great sporophytes probably stood in swamps or at least were hygrophytic in habit and by the requirements of their separated gametophytic reproduction could not exist on land areas independently.’ Reduced shoots and leaves are common enough at the present day among so-called ‘ swamp xerophytes ’ and are not necessarily an indication of a dry climate.

Among the Gymnosperms, however, the difficulty of a

separated gametophyte had been overcome and Bennettitales, Conifers and Cycads may have included many plants inhabiting semi-deserts as many modern Gymnosperms do. The Gymnosperms, however, do not exhibit anything approaching the same variety of growth form as the Angiosperms.

While it is reasonable to suppose that the more primitive forms of flowering plant are more likely to occur at the present day in the primitive unchanging types of habitat named above (tropical forest, stream-banks and marshy places, seashore and possibly mountains), it does not, as we have seen, follow that these habitats are exclusively occupied by primitive *families*, *genera*, and *species*. Many recent genera and species may retain ancient types of growth form.

But if, as is now generally believed, the grasses are a derivative group, grassland areas could not have existed until they were produced. There was nothing before them evolved that could exactly take their place, though *Equisetum* may have taken the place of reeds and rushes as Clements (' Plant Succession,' p. 350) maintains. Grassland habitats, dry scrub areas, semi-desert areas with succulents, and desert areas are all to be looked on as changing or derivative. Such of them as existed in palaeozoic times were almost certainly not dominated by Angiosperms, even if Angiosperms did occur then. The types of growth form produced amongst Angiosperms to suit these non-persistent or derivative types of habitat are themselves to be considered derivative.

It would seem, therefore, that we can now make an attempt to arrange growth forms in some sort of rough natural or evolutionary system, but the underlying guiding principles which we have outlined can be supported still further.

In naming and describing the primitive types of habitat some evidence was brought forward why their vegetation should be considered primitive, especially its very widespread character in each case. We have seen that the evidence from phylogeny cannot be held conclusive since recent types of flower may be borne by ancient types of growth form, but, as a matter of fact, it supports the conclusions reached in a very remarkable way.

Evidence from Phylogeny.—Different systematists according to their various viewpoints consider different families primitive. Taking first of all Engler's system, we find that the treatment of the Dicotyledons starts with *Casuarina*. Its possible connections with *Ephedra* have already

been referred to, and it has been found in fossil form in the lower Cretaceous (Comanchean) beds of North America. At present it occurs in the Australasian region and Indian Archipelago, with one species in Africa. *Casuarina* is a xerophytic genus of trees growing on sandy seashores, especially the widespread *C. equisetifolia*, though one species, *C. montana*, forms the xerophytic tjemoro savannah forest of East Java (Schimper, 1903).

Piperales.—These are herbaceous or shrubby forms considered primitive by Engler, though some consider that possibly they should be placed later in the sequence of families near the Polygonaceae (Gundersen, 1920). The Piperaceae, Chloranthaceae, and Lacistemaceae are tropical forest families; the Saururaceae are mostly swamp plants.

Salicales.—The two genera *Populus* and *Salix* both favour stream- and river-banks.

Myricales.—The only genus, *Myrica*, is usually a stream-bank or hygrophilous or seashore type.

Leitneriales.—The only genus, *Leitneria*, is found in salt or brackish swamps.

Batidales.—The only genus, *Batis*, is a seashore shrub.

We thus find that the seven of Engler's most primitive orders all belong to one or other of our primitive unchanging habitats, while, as we pursue his system further, we find that other relatively primitive 'orders' are preponderatingly tropical.

If now we turn to the larger order, the Ranales, which many consider to come nearer to the ancestral type of Angiosperm, we find greater variation. Some of the Ranunculaceae are herbs with highly evolved zygomorphic flowers, though even this family tends to favour marshy habitats. The climbing habit, which was probably very early evolved, is seen in *Clematis*. Of the other families, the Nymphaeaceae and Ceratophyllaceae are purely aquatic, while the Magnoliaceae, Menispermaceae, Anonaceae, Myristicaceae, Monimiaceae, and Lauraceae are mostly woody tropical or subtropical plants. It may be said that the vast majority of the Ranales also occupy primitive types of habitat, and it is not surprising that a few have become adapted to more modern drier conditions.

Among the Monocotyledons, the *Pandanales* are by many regarded as most primitive. Of these the Pandanaceae are trees and shrubs, sometimes root-climbers, widely distributed through the tropics of the Old World, especially in the islands

of the Indian and Pacific oceans. Species of *Pandanus* occur chiefly by the seashore, but also sometimes in forests.

The Typhaceae and Sparganiaceae are marsh or water plants, *Typha* being recorded from the Cretaceous.

The great series of the Helobieae are by many regarded as even more primitive than the Pandanales, since the Alismaceae possibly may connect with the primitive stock which gave the Ranales. Still others have considered a form like *Naias* primitive owing to the simplicity of its flower structure, which, however, is more likely the result of reduction. The whole of the Helobieae are aquatic, and many of them, like *Naias*, are world-wide in their distribution. The Potamogetonaceae are interesting because eight out of the nine genera occupy salt or brackish water, and only the largest genus, *Potamogeton*, has, on the whole, taken to fresh water. The family with its free carpels and solitary suspended orthotropous ovules is undoubtedly primitive. Of the fourteen genera of water plants belonging to the Hydrocharitaceae three, *Halophila*, *Enhalus*, and *Thalassia*, are marine. The life histories of the marine Angiosperms are dealt with in detail by Mrs. Arber (1920).

The small family of marsh plants, the Scheuchzeriaceae (Juncaginaceae) has the definite trimerous arrangement of the flower definitely established, the carpels being either free or united. *Triglochin* is the chief genus, and in tropical or subtropical regions at any rate has chiefly seashore or salt-marsh species, though elsewhere it grows in freshwater marshes. The genus *Lilaea* is of interest not only because it is somewhat grasslike in appearance with its sheathing leaves, but it also has a grasslike inflorescence and a caryopsis-like fruit. It is a marsh plant occurring along the mountain ranges of North and South America.

Among all the Helobieae, the Alismaceae, according to Mrs. Arber, are probably nearest to the ancestral stock. Their chief common character is the enlarged hypocotyl of the embryo, and Mrs. Arber suggests that not only do they connect with the Ranalean plexus, but they may have descended from a geophytic ancestor. The evidence to be drawn from phylogeny regarding the persistence of primitive types in primitive habitats is, I think it must be admitted, rather convincing.

An Outline of the Evolution of Growth Forms.—It is now possible to give, in a very general way, an outline of the probable course of ecological evolution. The following chapters of this

book will consist largely of the filling in of details as far as South Africa is concerned.

It is fairly certain that the tree form is among the most ancient of Angiosperms, and if the present-day tropical forests are nearest to the forests of Cretaceous times, then the most primitive types of woody plant were trees with simple leaves. All tree forms, however, are not primitive. Among the evolutionary tendencies have been : (1) reduction in size, (2) increase of branching leading to the shrub form, (3) reduction in size of the leaves, (4) increased branching in the leaf veins, (5) the production of compound leaves, (6) thorn development, (7) the development of succulence, (8) deciduous leaves, (9) general increase in xerophytism.

One tendency that seems to have appeared very early in the course of evolutionary history is the sclerophyllous, resulting in a marked increase in the amount of fibre in the leaves in species forming scrub, macchia, chaparral, etc. (Clements' class of Drymophytes).

Lianes, or climbing plants, are derivative but ancient (indeed the form is older than the Angiosperms), and have appeared again and again in different cycles of affinity. Herbaceous marsh types in general may be, like lianes, derivative within any special circle of affinity, or at least the herbaceous habit may not be so ancient among Angiosperms as the woody (as maintained by Sinnott and Bailey and others), but, as we have seen, the herbaceous type is very ancient. Like the climbing habit, it was evolved long before the rise of the Angiosperms. Purely aquatic forms among Angiosperms are probably always to be considered derivative.

The origin of the grasses is about the most important question in ecological evolution, and it will be discussed in greater detail in Chapter VII. It may very well be the case that among the Monocotyledons the Glumiflorae were the first to leave the marshy situations, moist forest margins, etc., and colonise the drier land surfaces, a task which they have accomplished very successfully.

The establishment of areas of grassland made possible the differentiation and multiplication of the types of plant-growth form adapted to grassland conditions, as well as great numbers of herbivorous animals. The plants that are associated with the grasses to form grasslands have usually underground storage organs, and as far as South Africa is concerned, where they are extraordinarily numerous, they are about

equally divided between Monocotyledons and Dicotyledons. Now, Miss Sargent's theory of the origin of Monocotyledons may be true, but the great development of such typical geophytes as the families Liliaceae, Amaryllidaceae, Iridaceae, and Orchidaceae, as we know them at the present time, could hardly have taken place before the origin of the grasses. The geophilous habit is also common enough among the Dicotyledons.

Parasites, saprophytes, and epiphytes are all dependent types of growth form which obviously would not be quite primitive. The same applies, though perhaps not to the same extent, to the herbaceous undergrowth of the forest. Undershrubs and suffrutices are derivative, though again possibly very ancient. It must for the present remain a matter of doubt just how ancient are the types associated with the forest but not dominant.

Not only for the trees and shrubs, however, but for all other types as well, as a general rule, increase of xerophytism has meant increased specialisation and relative evolutionary advance. Reduction in the transpiring surface is probably one of the first changes that would be undergone. This might be brought about by reduction in the size of the plant, or reduction in the size of the leaves, or both. Leaf division tends to serve the same purpose. Coverings to the leaf surface have not so much significance, but are again to be considered derivative.

The storing up of a water balance resulting in succulence is characteristic of many totally unconnected families and of large and important sections or genera of other families. In the latter case it is interesting to note that they are usually highly evolved floral types, e.g. *Euphorbia* in the Euphorbiaceae, the *Stapelia* section of the Asclepiadaceae, *Mesembrianthemum* in the Aizoaceae, and the most highly developed sections of the genus *Crassula*.

The evidence which I have summarised in a former paper (Bews, 1916) seems, on the whole, to support the views of Lothelier, Cockayne and others that thorn development is a response to dry conditions and only secondarily helps to protect plants against grazing herbivores. At any rate, thorny plants like succulents may be considered, in general, derivative rather than primitive, and in the South African flora this again serves as a most useful guide to evolutionary development within definite circles of affinity as in families

and large genera, some members of which have thorns and others not.

Most xerophytic of all, and therefore most highly evolved and recent, are the plants which produce seed quickly and then die, the Annual or Ephemeral class of growth forms (Raunkiaer's Therophytes). They are adapted to the most extreme desert conditions, where they are in the majority, as well as to conditions brought about by man's interference. Man has also been responsible probably for the wide distribution of most of them that are widely dispersed over the world as common weeds or ruderals.

It should be clearly realised that what has been outlined is to be considered the main general tendencies in ecological evolution. It is quite possible for the evolution of special types to run contrary to the main stream. Just as *Gunnera*, for instance, a marsh type, is supposed to have been derived from aquatic ancestors, though these are in general themselves derivative, so xerophytes may very well sometimes have given rise to mesophytes, hygrophilous types, or even hydrophytes. Mesophytes or marsh types also may have evolved in two or more directions, producing xerophytes on the one hand, and aquatic types on the other.

If we adopt Raunkiaer's system of life forms, the phanerophytes and helophytes are the most primitive, hydrophytes may often be ancient. Chamaephytes, hemicryptophytes, geophytes, and therophytes are, on the whole, derivative. Any system of arranging life forms should begin with the trees and shrubs and end with annual plants, but like all attempts at natural systems of arrangement a linear series is impossible. Each of the recognised groups has separate evolutionary tendencies and many xerophytic tree forms may be quite recent. Generally within each class of life forms xerophytic types are probably more recent than mesophytic and hygrophilous.

CHAPTER III

THE ORIGIN AND MIGRATIONS OF THE SOUTH AFRICAN FLORA

The Tropical-subtropical element—Seashore migration—Coast-belt migration—River-valley migration—Grassland types—The Temperate or Mountain element—The evidence from phylogeny.

1. The Tropical-Subtropical Element.—This is by far the most important in numbers and in area covered, occupying, as it does, the whole of South Africa except the south-western corner and the mountain ranges. For the evolution of the majority of the types of growth form belonging to it we may look not only to South Africa itself, but also to the tropical areas north of it, for within the tropics there are all gradations, from extremely high rainfall combined with high temperatures to extreme desert conditions also with high temperatures, or to cooler conditions with rising altitude on the tropical mountains combined with moderately high rainfall. At still higher altitudes on the tropical mountains the temperate element occurs. The rain-forest types of the tropics do not actually extend into South Africa, but hygrophilous subtropical forest is of an allied type. The true 'megatherm hygrophilous' forest occupies a large part of the Congo basin and particularly the western coast region from the mouth of the Congo right round to Bathurst and the river Gambia.

On the western side, according to Monteiro (1875), whose account remains one of the best I have read, 'this alternation of swamp and dense forest ends completely on arriving at the river Congo and a total change to the comparatively arid country of Angola takes place, in fact, at about 13° S. Lat. it becomes almost a perfectly arid, rocky and sandy desert.

'From the river Congo to Mossamedes no dense forest is seen from the sea and from thence not a single tree, it is said, for hundreds of miles to the Orange River. A little mangrove lining the insignificant rivers and low places in their vicinity is all that varies the open scrub of which the giant Adansonias

and Euphorbias have taken, as it were, exclusive possession. Nowhere on the coast is seen more than an indication of the wonderful vegetation or varied beauty and fertility which generally begins at a distance of from thirty to sixty miles inland.

'At this distance a ridge or hilly range runs along the whole length of Angola forming the first elevation; a second elevation succeeds it at about an equal distance, and a third at perhaps twice the distance again lands us on the central high plateau of Africa.

'At Quiballa, about sixty miles from the coast . . . the vegetation changes. Creepers of all kinds, attaining a gigantic size, clasp round the biggest trees and cover them with a mass of foliage and flower. No words can describe the luxuriance of these tree creepers, particularly in the vicinity of the shallow rivers and rivulets of the interior. Several trees together, covered from top to bottom with a rich mantle of Indiarubber creeper (*Landolphia*) with bright, large dark green leaves somewhat resembling those of the Magnolia, thickly studded with large bunches of purest white jasmine-like flowers, loading the air for a considerable distance with its powerful bitter-almond perfume and attracting a cloud of buzzing insects, form altogether a sight not easily forgotten. Once at Bembe I saw a perfect wall or curtain formed by a most delicate creeper, hung from top to bottom with bottle-brush-like flowers about three inches long; but the grandest view presented to my eyes was in the Pungo Andongo range where the bottom of a narrow valley for quite half a mile in length was filled, as they all are in the interior, by a dense forest of high trees; the creepers in search of light had pierced through and spread on the top where their stems and leaves had become woven and matted into a thick carpet on which their flowers were produced in such profusion that hardly a leaf was visible but only one long sea of beautiful purple, like a glacier of colour filling the valley and set in the frame of green of the luxuriant grass-covered hillsides.

'The comparatively short and spare thin leaves and delicate tufted grasses of the first or littoral region are succeeded in the second by much stronger kinds attaining an extraordinary development in the highest region. Gigantic grasses from five to sixteen feet high, growing luxuriantly, cover densely the vast plains and tracts of country where tree vegetation is scarce.'

I have quoted at some length because it gives a vivid and

accurate picture of tropical vegetation through the whole continent. With slight modification Monteiro's descriptions apply also to the eastern side. There is again the same mangrove vegetation on the coast, xerophytic tree-veld and scrub on the low-lying coast-belt, and, with rising altitude on the ascent to the central plateau, forest vegetation and tropical grassland. The forests of the eastern side differ floristically and ecologically from the western and Congo forests which extend eastward as far as Uganda, keeping more or less north of the main course of the Congo. All the great belt south and east of this Congo forest is more or less one floristic region, and a list of the known plants for Nyassaland and British territory north of the Zambesi, compiled by Burkill from the material in the Kew Herbarium for Sir Harry Johnston's work, 'British Central Africa' (1897), gives a good idea of its composition and its close relationship to the South African flora. This is the great tropical reservoir from which the subtropical element of the South African flora has been derived.

While the general migration has been southwards, it has not taken place uniformly or at a uniform rate. In our brief discussion of the climate of South Africa, it was shown that the effect of the warm Mozambique current on the eastern side as contrasted with the cold Benguela current on the western side was to bend southwards the isotherm lines on the east coast. Not only so, but from the Congo mouth southwards the whole western side is much drier than the eastern until it culminates in the coastal desert of the Namib. This, together with the great sand-veld area of the Kalahari, has interposed a barrier to the southward migration of hygrophilous and mesophytic types along the western side. Only xerophytic and derivative forms have invaded South Africa to any extent towards the west. The Karroo region, especially the western Karroo, may have received—and, as far as some of its elements are concerned (e.g. *Euphorbia* spp., *Mesembrianthemum* spp., etc.), doubtless did receive—some of its constituents from the west or directly through the Kalahari and upper basin of the Zambesi from the north.

The western escarpment of the central plateau is not so dry, and subtropical grasses allied to or identical with those of the eastern side are dominant, together with trees and shrubs and subordinate associated plants. Immediately south of the South-West Protectorate in the great valley of the Orange river there is interposed a very dry belt, and it is doubtful whether the

more mesophytic central and Karroo portions of South Africa received many at any rate of their relatively more mesophytic elements from this direction.

The main invasion of the subtropical Angiosperm flora into South Africa it would appear, therefore, has been along the eastern side. The various studies in detailed plant succession carried out in Natal have assisted in a clearer understanding of plant migration on the larger scale.

Seashore Migration.—The seashore is a uniform easy pathway leading to rapid migration of its own characteristic flora of strand plants, sand-dune species as well as mangroves and plants of the mud lagoons. Guppy has dealt in great detail with the question of seed dispersal among such types. Many species common on the shores of South Africa range all over the tropical seashores of the world ; others are local or endemic.

One of the most interesting lines of investigation is to observe how the purely tropical species decrease in numbers southwards as the warm sea-current on the eastern side loses its effect and the increasing influence of the cold currents from the south is felt. Only three Mangroves reach Natal. *Barringtonia*, *Hibiscus tiliaceus*, *Canavalia* spp., etc., are similarly checked in their southward migration. On the other hand, some of the strand plants, e.g. *Sporobolus pungens*, *Passerina* and others, extend round to or from the Cape.

Coast-belt Migration.—On the low-lying coast-belt away from the seashore migration has been much slower. Reference to any physical map of Africa will show that the 1000-foot coast-belt which is several hundreds of miles broad in Portuguese East Africa becomes narrowed like the neck of a bottle at Port Durnford in Zululand. Northwards from that point it is a broad flat sandy belt usually only 100 feet or so above sea level, but in Natal it becomes confined to a strip a mile or two broad along the coast-line. A considerable number of tropical species have not penetrated farther south than Zululand, and this may be due as much to the altered topography as to the general lowering of temperatures and change of climate. On the whole, however, slightly modified tropical or subtropical types have penetrated southwards to the limits of the south-western region in the Cape Colony, though in ever-decreasing numbers. The bulk of the Euphorbiaceous trees and shrubs, apart from the genus *Euphorbia*, stop at the eastern borders of the Cape Colony. So also the family Acanthaceae along the forest margins and as undergrowth gradually becomes less prominent. The Sapindaceae,

an essentially tropical family, has only a few species that have penetrated to the south-west region. The same applies to the Menispermaceae, Amarantaceae, Moraceae, Malpighiaceae, Scitamineae, Dioscoreaceae, Flacourtiaceae, Sapotaceae, Cucurbitaceae, Apocynaceae, etc., and other tropical families, their abundance in the tropics and their decreasing numbers southwards indicating fairly clearly their origin and history in South Africa.

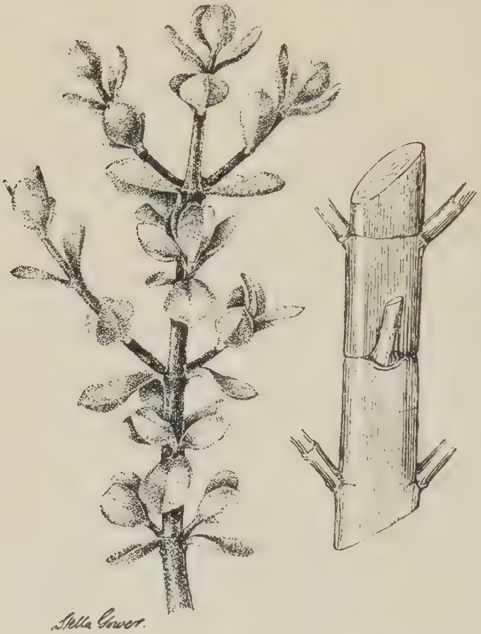

FIG. 1.—*Portulacaria afra* JACQ. $\frac{1}{3}$ nat. size. Abundant in eastern dry-valley scrub.

River-valley Migration.—While the maximum distribution of coast-belt species is in a line parallel to the coast, and their tropical affinities are close and obvious, their penetration farther inland has apparently always tended to follow the great river-valleys or the flanks of the intervening ridges. The more hygrophilous species migrate inland without much modification, remaining more or less close to the banks of the rivers and their tributaries, but away from direct influence of the water in the hot, dry river-valleys the vegetation is often of a highly modified xerophytic and derivative character. The coast-belt species themselves, however, include not only hygrophilous and mesophytic but also many xerophytic types. There are numbers of Acacias, Euphorbias, *Dichrostachys nutans*, etc. The last mentioned is a very typical coast-belt species and it has penetrated inland along the Tugela valley as far as the Lower Mooi river tributary. The mesophytic forest species occupy the rising slopes usually on the north side of each river-valley facing the rain-bearing winds. Plant-succession studies have shown

how tree growth of all kinds, so to speak, runs along the rivers and streams to begin with, then gradually spreads outwards. The pioneers of high forest are the species found in the fringe around its margin composed of light-demanding trees and shrubs. In the xerophytic valley scrub, on the other hand, as has been already explained, certain trees grow out as isolated pioneers through the grassland and either remain isolated or afterwards become the centres of clumps of more mesophytic species, which may ultimately kill the pioneer. This type of succession has been responsible for the covering of enormous areas of subtropical grassland throughout the continent with the parkland bush-veld or tree-veld type of vegetation.

The importance of the river-valley migration in South Africa was first of all suspected by observing the course of the plant succession over limited areas, but it has now been more fully tested by observing the maximum lines of distribution of rare or relatively rare species. In a former paper (Bews, 1922) I gave a list of no less than thirty-two of these for the Tugela valley alone, not one of which is known to occur in the next main river-valley of the Umgeni farther south. It is just those rarer species that throw a considerable amount of light on general questions of migration, and apart from the purely coast-belt flora the lines of the distribution of the rarer species in eastern South Africa tend to run at right angles to the coast. The dominant tree of many yellow-wood forests, *Podocarpus henkelii,* is a good example.

At the same time, among the commoner more widespread species, at similar altitudes in each drainage area the flora tends to be similar. As the foothills of the Drakensberg are approached the river-valleys are not so deep nor so dry and therefore do not form barriers to migration across them. The lines of migration are not clearly defined in this area, but the mountain ranges themselves are the main pathways of migration for their own peculiar flora, and their general direction in South Africa is parallel to the coast-line. River-valley migration on the eastern side runs only from the coast-belt up to the foothills of the Drakensberg, but farther south the highly modified xerophytic succulent and thorny scrub of the dry river-valleys reaches its most extensive development in the lower Fish river and through the great Addo Bush to beyond Uitenhage.

It contains succulent arborescent Euphorbias, Aloes, *Portulacaria afra*, etc., with much dwarfed forest and scrub

species—e.g. *Ptaeroxylon utile, Elaeodendron croceum, Apodytes dimidiata, Scolopia zeyheri, Sideroxylon inerme, Gymnosporia* spp., *Schotia latifolia, Capparis albitrunca, Maerua triphylla, Pappea capensis, Euclea undulata, Olea verrucosa, Rhus* spp.—and probably represents the source of the vegetation that clothes the Karroo kopjes.

FIG. 2.—*Gymnosporia buxifolia* L. ½ nat. size. Common pioneer in tree-veld.

In the central plateau and the western side the great Orange river and its tributaries afford a magnificent opportunity of studying river-valley migration, but unfortunately the numbers of migrating trees and shrubs are much smaller. The following are important: *Acacia karroo, A. giraffae, Salix capensis, Rhus lancea, Rh. viminalis, Royena pubescens, R. pallens, Zizyphus mucronata, Combretum erythrophyllum*, and in 'brak' places *Tamarix articulata.*

The river-valley migration of so many trees and shrubs is probably also to be correlated with the fact that the majority have fruits and seeds that are dispersed by animals. These move up and down the river-valleys which are their feeding grounds, but further study of the birds, antelopes and other mammals of South Africa from this standpoint is desirable.

Grassland Types.—The study of the migrations of the grasses and grassland plants of South Africa is much more difficult. They are usually wind-distributed, and they follow no such definite lines as the trees and shrubs. Nevertheless, a certain amount of information can be obtained from a careful study of their distribution. The general invasion of the tropical-

subtropical types has been from the north. The more tropical the grass-veld, the more definitely is it dominated by members of the great tribes Andropogoneae and Paniceae. *Themeda* is, of course, very widespread and the genus *Andropogon* is a very large one (now subdivided by Stapf into a number of separate genera). In the moister habitats species of *Cymbopogon* are prominent. The more tropical the grass-veld, the more common are species of *Panicum*, *Pennisetum*, and other members of the Paniceae. With increasing aridity, species of *Eragrostis* (Eragrosteae) and finally species of *Aristida* (Stipeae) become first of all common in the early stages of the plant succession and then dominant.

General Smuts has called my attention to the fact that the more tropical species are more prominent in any locality as the summer advances. In spring, while the temperatures are still low, the whole of the grass-veld has less of a tropical appearance and the purely South African derivative subtropical grasses are more in evidence. I have to thank him for permission to quote from a letter of his. After discussing the geographical succession, which I had been dealing with, he goes on: 'But what has struck me as strongly is the temporal succession in the same area. In spring, when the heat and rainfall are still moderate, it is the subtropical species which predominate and cover the view (*Eragrostis*, *Digitaria*, etc.). As the summer advances and the temperature and rainfall increase, the same area comes to be dominated by the tropical species (Andropogons, Cymbopogons, etc.) and the subtropicals practically disappear. This temporal or seasonal succession in response to the growing heat and rain is, to my mind, a wonderful thing and yet perfectly natural and understandable, proving how closely tropical and subtropical are associated in South Africa.' This valuable observation of General Smuts shows how it is possible, to a considerable extent, in a single area to compare tropical and subtropical floras and investigate evolutionary history by comparing the summer aspect societies and associations with those that precede them in the spring.

Associated with the grasses in the grass-veld and subordinate to them are an enormous number of herbaceous and half-shrubby perennial plants both Dicotyledons and Monocotyledons, and the study of their origins and migrations, though a difficult task, is full of interesting possibilities. The geophytic types, especially the bulbous and tuberous Monocotyledons, are most widespread and also most prominent in

spring. While the species are often very local, the larger genera have spread all over South Africa and are prominent in the mountains and south-west, as well as in the subtropical areas. The autumnal aspect societies are more shrubby, more tropical, compete more directly with the grasses, and are sometimes transitional to scrub in the forest areas. The general evolutionary tendencies of the associated plants of the grass-veld, however, have been in the direction of increased xerophytism, increased underground storage—not only of food but also of water, the latter being perhaps the more important—increased succulence, etc. In the transitional Compositae Veld of the central areas the associated plants become more and more prominent, competing successfully with the xerophytic grasses (Aristidas, etc.) until finally on the Karroo plains the dwarf shrubs and succulents become completely dominant with highly specialised types of bulbous plants, etc.—e.g. *Eriospermum* spp.—associated. The extraordinary capacity for rapid assimilation on the part of these plants while conditions are favourable will be referred to more in detail later, but there is room for much interesting comparative physiological work in connection with these studies of migration.

The Karroo has derived its constituents partly from the shrubs of the eastern xerophytic scrub, partly from the xerophytic associated plants of the grass-veld, partly from xerophytic grasses themselves, and the whole, highly modified and specialised, represents the final result of plant evolution and the last stage in plant migration in South Africa. How very specialised its flora is will be understood more fully when its many weird growth forms are dealt with in detail.

2. The Temperate or Mountain Element.—The general distribution of this element has already been given. It extends from the mountains of Abyssinia through the central tropical mountains of East Africa (Kenia, Ruwenzori, Kilimanjaro) to the mountains of eastern South Africa and across to the south-western region of the Cape where it descends to the sea level. In the south-western region it is by far the richest in genera, species, and endemics. The representatives on the eastern and central mountains, though they mix with the subtropical flora and are relatively few in numbers, are not rare or sparsely scattered, but, on the contrary, often dominant in the plant associations. The temperate African flora, however, was first known and described from the Cape, and the mountains even now remain only partially explored. It is natural, therefore, to

speak of the eastern and central temperate genera and species as 'outliers' of the richly developed, well-known south-western flora. Such a term tends to assume an origin for the temperate flora in the south, and this assumption may be right, though it does not follow that the region where a flora is now best represented is necessarily the centre or nearest to the centre of its origin. The temperate and mountain flora of Africa shows certain connections with the flora of the temperate regions of the northern hemisphere. The genus *Erica* is the largest in it, and it has spread all over the north, while there are many other genera as well which extend from the Cape to Europe. On the other hand, the Proteaceae, Restionaceae, and smaller families, as well as many genera of Compositae, Gramineae, Rutaceae, etc., are confined to it, though it is doubtfully claimed that the Proteaceae at one time occurred in Europe. The northern connections are, on the whole, sufficiently clear, but very few species are common to the two floras, neglecting, of course, those introduced from one to the other by man. The connecting line across Central Africa is a very broken one, with much reduced numbers of temperate families, genera, and species.

Two opposing views regarding the origin of the temperate African flora have hitherto been held by different botanists. The one looks upon the south-western flora of the Cape as the remnant of an Antarctic flora now represented also in Australia and the extreme south of South America. If Waegener's theory of continental drift were established, it would lend considerable support to this view. The breaking up of the land areas in the southern hemisphere has simply resulted in the separating of floras once joined together in one area with a temperate climate. The outliers on the tropical mountains are representatives that have pushed northwards to a greater or less extent. This appears plausible as applied to such a genus as *Protea*, but in other cases there are difficulties. Such questions as the following might be asked: Have the Ericas of Europe all come from the Cape where there are now nearly 500 species existing? What explanation (if we accept a southern origin for the Cape flora) can be offered of the families or genera now represented by a few species at the Cape and a great many in the northern hemisphere?

The second theory of the origin of the temperate flora of South Africa is supported by Thiselton-Dyer, Guppy, and others. It is a theory of southward migration from the northern

hemisphere. It postulates a relative permanency of the general configuration of the land masses of the earth's surface, a view in agreement with those of Darwin and Wallace, but, to a certain extent, at variance with those of Hooker, who was more inclined to postulate great geographical changes.

As Guppy puts it, ' If it can be shown, as undoubtedly the general trend of the facts of distribution does show, that the divergence of plant types responds to the divergence of land masses from the north and that dissimilarity is intensified with distance from that pole, any evidence for a Tertiary Antarctic centre for the flowering plants would be discounted in advance.'

Thiselton-Dyer and Guppy agree that centrifugal dispersion of species from the north, which all acknowledge took place during the last Ice period, has been repeated often in the course of geological time.

' At a time when a genial climate prevailed over the northern or land hemisphere, the plants now represented in type in the warmer latitudes occupied the regions beyond the Arctic Circle. When this period gave place to cooler conditions, the retreat to the South began : and the plants, as the diverging continents pulled them more and more asunder, became more and more distinct from each other. . . . When the warmer conditions returned, the plants advancing northwards met again in the common gathering ground around the Pole but modified by their different experiences in southern regions lying oceans apart. There they mingled together, the eastern and the western floras, and when, with the next climatic change, they began again to retreat to their ancient home in the warmer latitudes of the south, the east had borrowed from the west and the west from the east. The secular changes of climate have, therefore, tended in this way to mix together the floras of the globe.'

Thiselton-Dyer speaks of the southern end of South Africa as a ' cul-de-sac into which the species have poured and from which there is no escape ' ; hence the extraordinary congestion of species there.

I have discussed these and other views in a former paper (1921), and one criticism made to me afterwards by one of our foremost South African botanists was, ' Plants do not behave like a flock of sheep.'

According to this second view the primitive ancestors of the whole temperate and south-western flora of Africa came from the north, but they have left few descendants along the track of their invasion because conditions there are not generally

suited to them. When they reached more temperate areas in South Africa they multiplied exceedingly and produced many divergent types in the course of their differentiation. The south-western flora is now a very rich and interesting one in consequence, containing an enormous assemblage of endemic forms.

This view affords a reasonable explanation of the distri bution of families at the present day common to the northern hemisphere and the Cape, and even such genera as *Erica* that are much better represented in South Africa than in Europe.

At the same time, it is hardly so convincing when the distribution of such families as the Proteaceae, Restionaceae, Penaeaceae, and Bruniaceae is considered. The bonds of affinity between the three floras—Australian, Antarctic, and South African—are scarcely sufficiently explained by it.

When two opposing views are each supported by what appears to be sound arguments the natural solution is a compromise, but there are other possibilities to be considered. Multiple origins or polygenesis is always possible, and there is no reason why many of the widespread elements of the African temperate flora may not have several centres of origin. The question is bound up with the origin of the temperate flora as a whole. Sinnott and Bailey have already been referred to. They have brought forward much evidence from palaeobotany, anatomy and phylogeny, as well as from geographical distribution, to show that the tropical woody type of plant is an older form than the temperate herbaceous type, so that the temperate flora, like the subtropical, is probably in general derivative. At the same time the temperate flora is undoubtedly very ancient, as can be seen when we consider the following facts :

(1) It is the most widely distributed over the world, occurring in both northern and southern hemispheres and crossing the equator by the mountains of the tropics.

(2) It has become very highly differentiated.

(3) It shows no close connections with the tropical flora. If it has been derived from a tropical or subtropical flora it must have had an origin almost as ancient as the Angiosperms themselves.

(4) Evidence from phylogeny, which we are going on to discuss, tends to show that in South Africa the temperate flora is, in some respects, of an older type than the subtropical with which it comes into immediate contact. The subtropical flora,

to a large extent, may reasonably be supposed to have been derived from the tropical in comparatively recent geological time. This cannot be said of the temperate flora.

The Evidence from Phylogeny.—The general evidence from phylogeny supporting the views set forth in the last chapter regarding the evolutionary history of growth forms applies to their migrations into South Africa and need not be repeated here. Instead of that, separate families will be considered only in so far as they are represented in the continent of Africa. It is impossible to deal with them all, but as representative a selection as possible has been made. The evidence is very strong in support of the view of a southward migration for the tropical-subtropical flora, and there are also indications of the rather ancient character of the south-western flora, but at the same time it is not impossible that some types may have originated in extra-tropical regions and have, in their turn, invaded the tropics as apparently has happened in the case of the large family, the Compositae, if we deal with its distribution in the world as a whole. In the arrangement of the families considered, Engler's system is followed, but the Dicotyledons are dealt with first.

MORACEAE.—The sub-family Moroideae are all tropical, with what is perhaps the most primitive tribe (the Fatoueae) represented by one monotype, *Bleekrodia*, in Madagascar. Of the central tropical African genera, *Dorstenia* with its flat-expanded receptacles has fifty species. The sub-family Conocephaloideae (*Musanga*, *Myrianthus*) are also tropical and have the ovules erect and straight—a primitive character. The other sub-families have the ovules pendulous, curved or inverted, and though the majority are still tropical, they include the large genus *Ficus* with its highly specialised type of inflorescence. It has 160 African species and a considerable number of them have migrated southwards, chiefly along the coast-belt of Zululand and Natal and inland, always along the river-valleys. The herbaceous *Cannabis* has probably been introduced into South Africa.

SANTALACEAE.—*Exocarpus* (one species in Madagascar) is relatively primitive in having the ovary superior; the South African genera have the ovary inferior. The herbaceous hemi-parasitic genus *Thesium* is by far the largest and at the same time most highly specialised.

LORANTHACEAE.—*Loranthus* is distinctly more tropical than *Viscum* and has a less modified type of flower.

Amarantaceae.—The tribe Celosieae, with ovules two or more, are tropical and East African. The tribe Amaranteae, which have the ovules reduced to one, are widespread and include several tropical and eastern genera, but have produced many genera characteristic of or endemic in the drier western side (Angola, Hereroland, Damaraland, and Namaqualand).

Aizoaceae.—The tribe Mesembrianthemeae, with the ovary inferior, represent the highest development in the family and are most characteristic of the Karroo and western highly specialised flora.

Menispermaceae.—The South African genera *Cissampelos* and *Antizoma* have the petals and sepals reduced in number, the stamens united, and the petals of the male flowers united, more advanced in every respect than the other twenty-five tropical genera.

Connaraceae.—All the twelve genera are tropical, with one South African species, *Cnestis natalensis*, a climbing plant.

Rosaceae.—Largely temperate rather than subtropical, and the tropical sub-family in this case has often irregular flowers (the Chrysobalanoideae) showing relative advance. The tropical types, however, have retained their woody character.

Leguminosae.—(*a*) Sub-family Mimosoideae. The tribes Parkieae, Mimoseae, and Adenanthereae are all relatively primitive in floral structure and all tropical or North African except *Dichrostachys*. *Acacia* is the great subtropical genus, a xerophytic tree type, usually (in Africa) thorny. (*b*) Sub-family Caesalpinoideae. These are relatively primitive in floral structure and woody and are mostly tropical, with outliers in South Africa (*Bauhinia*, *Parkinsonia*, *Burkea*, *Cassia*, *Umtiza*, *Schotia*). (*c*) Sub-family Papilionatae have highly developed floral structure and are more often herbaceous. They are chiefly subtropical and temperate. The relatively primitive tribe, the Podalyrieae, with the filaments free, are mostly south-western—one of the indications of the relatively ancient character of the south-western flora as compared with the subtropical but not as compared with the purely tropical.

Erythroxylaceae.—The equatorial West African *Aneulophus* has an ovary with three to four two-ovuled cells. *Erythroxylon*, which extends into South Africa, has the ovary with one fertile one-ovuled cell and two empty ones, showing advance.

Rutaceae.—The sections Toddalioideae and Aurantioideae consist of trees and shrubs with fleshy fruits and are tropical

or eastern. The Rutoideae are shrubby or herbaceous, with dehiscent more or less dry fruits, and include all the temperate and south-western genera together with *Fagara* and *Calodendron*, which are eastern.

Burseraceae.—*Commiphora*, the only genus which extends into South Africa, has the receptacle concave instead of flat or convex; relatively an advanced type.

Polygalaceae.—The tropical genera *Carpolobia* and *Atroxima* have all the five petals well developed, unappendaged, and the ovary two- to three-celled, and are more primitive than the South African genera *Muraltia*, *Mundia*, and *Polygala*.

Euphorbiaceae.—The tribe Euphorbieae, with ovules one in each ovary cell, milky latex and highly modified flower-like partial inflorescences, are in every way the most highly developed, and at the same time, within the limits of the large genus *Euphorbia*, show the greatest amount of adaptation to drier extra-tropical conditions. Within the section the relatively primitive genera *Anthostema* and *Dichostemma* have male flowers with a perianth and are tropical. *Elaeophorbia* (West Africa) has the fruit a drupe, while *Euphorbia* has a capsule.

Anacardiaceae.—The tribe Spondieae, with three to five fertile cells in the ovary, are more distinctly tropical than the tribe Rhoideae, which include *Rhus*. The genus *Protorhus* is mainly in Madagascar. The single Natal species, *Protorhus natalensis*, is an interesting transitional type which does not agree altogether with the characters of the genus. *Protorhus* has simple leaves. The more subtropical *Rhus* has trifoliate leaves.

Violaceae.—The tropical-subtropical Rinoreae (shrubs or trees with regular flowers) are more primitive than the subtropical and temperate *Violeae*, herbs with irregular flowers.

Flacourtiaceae.—The tribe Erythrospermeae, with the perianth leaves spirally arranged, the sepals gradually passing into the petals, and the ovary superior, are widespread in the tropics, with one genus, *Rawsonia*, reaching Natal. The other nine South African genera are more advanced in flower structure, having the perianth leaves whorled and the sepals separated from the petals or the petals absent.

Thymelaeaceae.—*Octolepis* is the most primitive type, with a flat receptacle and the ovary four- to five-celled. It is purely tropical (seven species in West Africa). *Peddiea* is

an East African tropical-subtropical genus of small trees with a two-celled ovary and the fruit a drupe, not so primitive as *Octolepis*, but more so than all the other South African genera of shrubs, undershrubs and herbs, which have the ovary one-celled (*Gnidia*, *Passerina*, *Lachnaea*, etc.).

Combretaceae.—*Strephonema*, a West African genus, is most primitive, with the ovary only half inferior. In the Combretoideae, which include the South African genera, the ovary is wholly inferior and the fruit usually angled or winged.

Araliaceae.—Tropical-subtropical and a few temperate trees and shrubs contrast with the Umbelliferae, which are mostly herbs, subtropical and temperate. *Heteromorpha arborescens* is, however, an interesting tree umbellifer from Natal, found usually at higher altitudes.

Myrsinaceae.—The genus *Maesa*, which is common in open rocky places in Natal, shows relative advance in having the ovary inferior or half inferior instead of superior as in the rest of the family. The Myrsinaceae contrast with the Primulaceae, which are herbaceous and derivative.

Loganiaceae.—The sub-family Loganioideae are more tropical and more primitive than the Buddleioideae.

Apocynaceae.—Mostly tropical-subtropical trees and shrubs having more primitive types of floral structure than the highly specialised Asclepiadaceae, which are subtropical and temperate. Within the Asclepiadaceae there are interesting stages of differentiation. The Periplocoideae, with loose pollen, are more tropical than the Cynanchoideae. The climbing habit has been adopted by different tribes. A large number are geophytic and adapted to grassland conditions, and the most highly specialised of all, the tribe Stapelieae, are especially characteristic of the Karroo and drier areas of the western side of South Africa.

Borraginaceae.—The tropical-subtropical Cordioideae and Ehretioideae, trees and shrubs, have the styles inserted at the apex of the ovary and are distinctly more primitive than the Borraginoideae, subtropical and temperate shrubs, undershrubs and herbs. The whole of the Labiatae are also allied and derivative.

Verbenaceae.—Here the sub-family Stilboideae are in some respects, *e.g.* the endospermous seeds and in several genera regular corollas, the most primitive and they are south-western. They have, however, basal inverted ovules as against the straight or half-inverted ovules attached laterally in the tropical-

subtropical sub-families Avicennoideae, Caryopteridoideae, Chloanthoideae, and Viticoideae.

Zygomorphy in the corolla appears to be quite as characteristic of tropical forms as of subtropical and temperate. It is, after all, somewhat of a superficial character in floral evolution and is characteristic of primitive as well as advanced forms.

Solanaceae.—The central African tribe Salpiglossideae (*Schwenkia*) show advance in superficial flower structure by the reduction of the stamens to two (rarely four).

Scrophulariaceae.—The family, as a whole, is itself derivative, subtropical and temperate, and has become differentiated in several interesting directions. A few are trees, e.g. *Halleria,* and these are tropical-subtropical. *Bowkeria* has developed compound leaves and is characteristic of open scrub and rocky places in South Africa. *Dermatobotrys* is epiphytic. Water and marsh forms (*Limosella*, *Diclis*) are very widespread. A large number of grass-veld genera are hemiparasites and some are holoparasites, e.g. *Harveya* and *Hyobanche.* The Selaginaceae are a derivative family, sometimes included as a tribe, subtropical and south-western. The Pedaliaceae are another derivative family, especially characteristic of the drier western areas or occurring as weeds. Other derivative families are adapted to special habitats or modes of life, *e.g.* Orobanchaceae (parasites), Gesneraceae (epiphytes and forest undergrowth), Lentibulariaceae (aquatics and often carnivorous).

Acanthaceae.—Tropical and subtropical as a whole, but the more primitive types (*Thunbergioideae*) are more tropical than the Acanthoideae.

Rubiaceae.—The Cinchonoideae, with two or more ovules in each ovary cell, are, on the whole, more tropical than the Coffeoideae, where the ovules are solitary, but in both sections the trees are more tropical and subtropical than the herbaceous forms, e.g. *Oldenlandia* in the former section, and *Galium*, *Rubia*, *Hydrophylax*, and *Richardsonia* in the latter.

Compositae.—The south-western and mountain genera of this largest family are most often woody and in other respects are rather primitive. The family is abundant in the grass-veld and becomes dominant in the transitional areas between grass-veld and Karroo as well as in much of the Karroo itself, but these forms are relatively more highly specialised than the mountain types. The family is relatively rather rare in

the tropics, though in subtropical forest it has produced some climbing species, e.g. *Senecio* spp. and *Mikania* spp. Small's work should be consulted for further details.

This general survey of Dicotyledonous families could have been expanded to almost any length, and in itself it represents one of the lines of investigation most full of promise for African botanists. The whole of the evidence consistently supports the views set forth regarding the origin and migrations of the South African flora. The tropical flora is, on the whole, within each family or circle of affinity, the oldest, the subtropical is derivative, and often the evolutionary lines are very clear, especially when the more essential flower characters are considered—the stamens, ovary, and ovules. Zygomorphy, however, and other floral characters more directly concerned with insect visits are often most highly developed in the tropics. There are a few indications that the temperate flora, while not so old as the tropical, is more so than the derivative subtropical, and, in some cases, families of extra-tropical or mountain origin, like the Compositae, have in turn invaded the tropics. There is very little evidence, however, of this northward invasion into the tropics having occurred to any great extent from South Africa, unless we include the typical Cape families which have outlying representatives on the mountains of Central Africa. This question has already been discussed.

The distribution of the Monocotyledons in Africa, to a certain extent, shows the same features as the Dicotyledons. Some primitive families are all tropical, *e.g.* the Pandanaceae, or are mainly tropical with subtropical extensions, *e.g.* the palms and aroids. The primitive aquatic or semi-aquatic families belonging to the Helobieae tend to be very widespread, and the study of their distribution throws little light on their phylogeny. Among the Glumiflorae the relatively more primitive Cyperaceae are also widespread and are mostly marsh forms. According to Schönland (1922) some of the most primitive genera belong to the south-western region in South Africa. The origin of the more specialised Gramineae is still obscure, but while the Bamboos, which are chiefly tropical, have a rather more primitive type of floral structure, the spikelets of other large tropical groups, the Andropogoneae and Paniceae, are rather highly specialised.

The Liliiflorae are interesting in that the central family, the Liliaceae, are very widespread and are most highly

differentiated as far as growth forms, etc., are concerned, while among the derivative Iridaceae the probably most primitive Aristinae have their chief centre at the Cape, but have two genera in tropical and subtropical America.

The most highly specialised of the Orchids are tropical.

On the whole, the Monocotyledons, in their distribution, do not show very clear indications of their history. An explanation of this might be obtained if we are prepared to assume that the early Monocotyledons were marsh forms and, like modern marsh and aquatic plants, tended to become widespread rather quickly. Those of the Monocotyledons which, like the majority of the Dicotyledons, had a tropical origin, show more clearly their evolutionary history when their distribution is analysed.

The more evolution has been controlled and influenced by climatic differentiation the more clear the record is, but, as we have seen, marsh and aquatic plants are largely independent of climate and their evolution has not been much affected by climatic changes.

CHAPTER IV

THE TROPICAL-SUBTROPICAL TREES AND SHRUBS

The Mangroves and Barringtonia association—Hygrophilous forest types—Mesophytic forest and scrub types—The evolution of the shrub form.

This class of growth forms in South Africa may be subdivided into three main sub-classes, and these in turn fall into various ecological groups depending on differences of habitat.

First of all, there are a number of hygrophilous trees which grow along stream-banks and in other moist situations, and in their general growth-form characters and rather large simple leaves approach very close to the megatherm hygrophilous forest trees of the tropics. Allied to these are the Mangroves, Barringtonia, etc., of the river mouths and mud lagoons.

The second class is a larger one, consisting of the trees and shrubs which compose the high forests of eastern South Africa, types rather mesophytic in most features, somewhat xerophytic in others, and allied to the forests of East African mountain slopes within the tropical area. The third class is much more heterogeneous, showing increase of xerophytism in various directions, showing great diversity in growth form, adapted to open tree-veld conditions, in habitats which are sometimes mesophytic, sometimes very xerophytic, and sometimes forming succulent and thorny scrub. The evidence we have already given tends to show that the third class is, to a large extent, derivative.

The dwarf shrubs and suffrutices adapted to grassland areas and Karroo or desert are not included in this class, though in many cases they may be fairly clearly connected, and are also derivative.

The Mangroves and Barringtonia Association.—These sea-shore types as represented in South Africa are simply outliers of the tropical flora, and may therefore be dealt with first of all by themselves.

The Mangroves of Portuguese East Africa belong to a variety

of families. From Delagoa Bay northwards, near every river mouth and inland along the rivers, often for many miles, the following occur:

Rhizophoraceae: *Rhizophora mucronata*, *Bruguiera gymnorhiza*, and *Ceriops candolliana*.

Combretaceae: *Lumnitzera racemosa*.

Lythraceae: *Sonneratia acida*.

Sterculiaceae: *Heritiera littoralis*.

Meliaceae: *Carapa moluccensis*.

Verbenaceae: *Avicennia officinalis*.

Of these only three extend southward through Natal to Pondoland, viz. *Rhizophora mucronata*, *Bruguiera gymnorhiza*, and *Avicennia officinalis*. All three are very widespread eastern Mangrove types.

The Mangroves are of great botanical interest from many standpoints, and there is an extensive literature dealing with them. References will be found in Schimper (1903) and Guppy (1906), both of whom devoted special attention to them. Schimper deals with their well-known adaptations to their habitat conditions, the salt or brackish water and badly aerated mud in which they grow their stilt roots and breathing roots, and sums up their leaf characters as follows: 'The leaves possess a marked xerophilous structure with a thick cuticle, large mucilage cells, protected stomata and especially a large-celled, thin-walled aqueous tissue, the dimensions of which increase with the age of the leaf and with the corresponding rise in the amount of salt contained. Old leaves serve essentially as water reservoirs for the younger leaves.'

Experiments on our Natal species have shown that the aeration system of the leaves is relatively well developed (from 20 to 30 per cent. of the total leaf volume), and there is little variation or plasticity in this respect (see Bews and Aitken, 1923). Probably most of their physiological functions show a narrow range of variation, since their habitat is very uniform. Guppy (1906) has studied carefully their reproduction, in which chief interest is centred in their habit of vivipary. Vivipary is not confined to the Mangroves. It occasionally occurs in many other plants. Instances are given by Goebel (1889), such as Wheat, Cacti, *Epilobium*, *Agrostemma*, *Juncus*, and the Borneo Camphor-tree, *Dryobalanops camphora*. Guppy mentions also the Mandarin orange, the Papaw, species of *Hibiscus*, *Croton*, *Ipomaea*, *Luffa*, etc. In abnormally wet years some of our

South African grasses show abnormal vivipary, e.g. *Eragrostis brizoides* (illustrated in my ' Grasses and Grasslands of South Africa,' p. 118).

On such facts as these Guppy has based an interesting theory. In the occasional cases of incomplete vivipary occurring among inland plants, and in the singular structure presented by the seeds of certain genera of Myrtaceae and other orders, he perceives indications of a lost viviparous habit belonging to a primeval period when the sun's rays were screened off by a dense cloud-covering that enveloped the earth, and the atmosphere was ever charged with moisture. ' With the differentiation of climate that has marked the emergence of the continents during the secular drying of the earth, the viviparous habit has been alone retained within the confines of the mangrove swamp, where the conditions once almost universal now survive; and as an adaptation to the differentiation of climate and to the resulting seasonal variation the rest period of the seed has been developed.'

Barringtonia racemosa (Lecythidaceae) is dominant in wet sandy soils near the river mouths where the water is fresh or rarely slightly brackish. It is a tree with dense heavy foliage. Its leaves are simple and from five to ten inches long when fully developed. They are of a common tropical type with a stout midrib and pinnately arranged lateral veins. The smaller veinlets enclose relatively large ' islands ' of assimilating and transpiring tissue, a feature in which it agrees with many other hygrophilous tropical-subtropical species (for an illustration, see Thonner, 1915, Plate 111). *Barringtonia* is common and widely distributed near tropical seashores. It is commonly associated with another very widely dispersed seashore species, *Hibiscus tiliaceus*, the leaves of which are roundish cordate, up to six inches or more long and wide, on long petioles, somewhat leathery, but the islands of tissue again fairly large. *Thespesia populnea* belongs to the same family (Malvaceae), and has leaves very similar to those of *Hibiscus tiliaceus*, with which it occurs near the sea in Portuguese East Africa.

In Natal *Eugenia cordata* (umDoni) often is found in the *Barringtonia Association*, but occurs inland as well.

Hygrophilous Forest Types.—The growth forms of these are not modified in the direction of the ' physiological xerophytism ' shown by the Mangroves and other seashore species, and they therefore approach most nearly the types found in

moist tropical forest. At the same time they are not merely outliers of a purely tropical vegetation, but are, on the whole, derivative types more distinctly South African. They show

FIG. 3.—*Xymalos monospora* BAILL.
$\frac{1}{3}$ nat. size. Hygrophilous forest tree throwing very dense shade.

gradations of xerophytism in response to increase of drier conditions. As already explained, they occur near water and migrate along the stream and river banks. Though they are

to a certain extent independent of climate, yet the climate has an effect, and true hygrophilous forest does not occur in the drier climatic areas where it is replaced by scrub which is often very xerophytic, thorny or succulent. Of course, the presence of abundance of water in the soil modifies the effect even of a very dry climate. More mesophytic species occur near the river-banks than elsewhere in the dry river-valleys, and over large areas of the Karroo and western side the only tree growth of any kind occurs along the river-beds.

The habitat of hygrophilous forest as distinct from scrub of various kinds cannot therefore be defined simply on edaphic lines as a stream- and river-bank habitat. This must be combined with the moister types of summer rainfall climate. Hygrophilous forest species, as thus defined, occur at various altitudes from the eastern coast-belt up to the Drakensberg. Some of the species, however, are confined to the coast-belt, while the majority have migrated to a greater or less distance inland.

The following may be taken as representative: Moraceae: Various species of *Ficus*, especially *Ficus capensis*, *F. nekbudu*, *F. capreaefolia*, and *F. natalensis*, are characteristic but not altogether confined to the habitat. The last mentioned usually begins life as an epiphyte, ultimately killing its host and itself forming a large tree. The genus shows various degrees of increasing xerophytism, some of the species being reduced to small shrubs. The leaves are rather large, smooth-margined, usually leathery, with sunk palisade tissue.

Monimiaceae: *Xymalos monospora* (Lemonwood) (see Fig. 3). This tree is dominant or subdominant in many of the moister midland forests of Natal. It throws exceptionally dense shade and there is little or no undergrowth beneath its canopy. Its leaves are simple, somewhat leathery, dark green in colour, with rather large reticulations in the veining and a somewhat uneven surface; a common tropical type. The genus *Chloropatane* of equatorial West Africa differs in having the leaves alternate instead of opposite.

Euphorbiaceae: *Antidesma venosum* has thinly coriaceous or membranous leaves up to 6 inches long by $2\frac{1}{2}$ inches wide, varying from thinly pubescent to tomentose underneath. *Bridelia micrantha* has leaves which vary from 2 to 7 inches long and 1 to 3 inches wide. Tertiary nerves are inconspicuous. *Macaranga capensis* (Fig. 4) has leaves up to 6 or more inches long and 4 or more inches wide, 3- to 5-nerved

from the base with 7 to 9 secondary nerves on each side above the base, the nerves all raised on the under side. The ultimate reticulations are small. The study of the nervation in leaves of the Euphorbiaceae shows a general tendency

FIG. 4.—*Macaranga capensis* BTH.
½ nat. size. Hygrophilous coast-belt tree.

towards the production of smaller and smaller islands of tissue between the small veinlets, with increasing xerophytism, though the above all belong to the hygrophilous habitat.

Croton spp. have the leaves usually beset with stellate hairs or orbicular scales. *Croton sylvaticus* is rather hygrophilous. *Sapium mannianum*, a coast-belt tree with membranous or

thinly coriaceous leaves up to 6 inches by 2 inches, is also to be included in this class.

Apocynaceae: *Voacanga dregei* has leaves 4 to 6 inches by 1 to 2 inches, subcoriaceous, with slender almost horizontal secondary nerves. *Conopharyngia ventricosa* is similar, with leaves sometimes slightly larger (see Fig. 5). Both species are common in coast-belt hygrophilous forest. *Rauwolfia natalensis* is more a Midland Natal species, often dominant in stream-bank bush or forest. The leaves are narrower, 3 to 8 inches long by $\frac{3}{4}$ to $1\frac{1}{2}$ inches broad (see Fig. 6). There are 20 to 30 secondary sub-horizontal nerves on each side of the midrib. These three illustrate a distinctive tropical type of leaf, with a single midrib and numerous sub-horizontal or oblique slender side veins, all more or less parallel. The tertiary veinlets and small reticulations are much more conspicuous in *Rauwolfia* than in the other two, and *Rauwolfia* by its distribution at higher altitudes inland shows a more distinct South African, subtropical and derivative character than *Voacanga* or *Conopharyngia*, which are entirely confined to the frost-free, almost tropical coast-belt. The comparison here again illustrates an important evolutionary process in response to increasing aridity and lower temperatures.

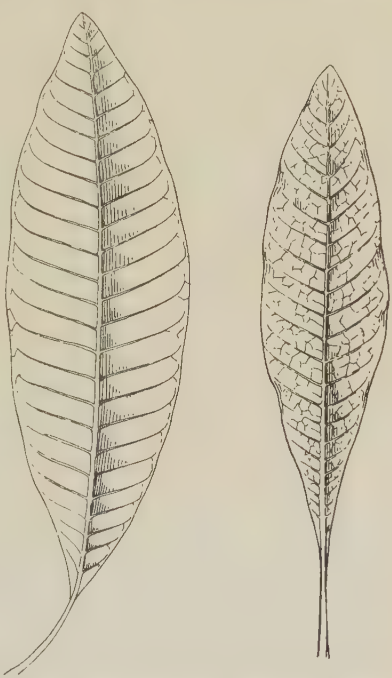

FIG. 5.—*Conopharyngia ventricosa* STAPF (to the left) and *Rauwolfia natalensis* SOND. (to the right).

Both $\frac{1}{2}$ nat. size. Note increased branching of leaf veins and decreased size of *Rauwolfia*.

Eugenia cordata (*Syzygium cordatum*) (Myrtaceae), the um-Doni, is often dominant in the more open types of coast-belt hygrophilous bush.

There are a number of other species belonging to various families which often or usually occur in hygrophilous forest, but are not confined to it, e.g. *Combretum kraussii*, *Combretum*

salicifolium, *Pittosporum viridi florum*, *Rapanea melanophleos*, *Protorhus longifolia*, *Clerodendron glabrum*, *Celtis rhamnifolia*, *Ilex mitis*, and *Dactylopetalum verticillatum*, all with simple leaves, usually leathery (or coriaceous) and with finely reticulate venation.

FIG. 6.—*Rauwolfia natalensis* SOND.
½ nat. size. Common stream-bank tree in Natal midlands.

Species with compound leaves are very rare in this class. *Albizzia fastigiata* and *Erythrina caffra* sometimes occur in it. In compound leaves the separate leaflets are the assimilating and transpiring units, and these may be large enough to compare with the whole leaves of other species (*e.g.* in *Trichilia emetica*), *Erythrina* spp. and others.

Hygrophilous forest species in South Africa agree in having leaves which, on the average, are considerably larger than the average for the group of South African trees and shrubs as a whole. A very small percentage have compound leaves. With the exception of *Rhamnus zeyheri*, which occasionally is found, there is no thorn development and there is an entire absence of succulents.

There are, however, certain tendencies towards xerophytism. The leaves are not, as a rule, thin and membranous. Evergreen leaves of trees rarely are. But the leathery or coriaceous texture seen in various Euphorbiaceous species, *Xymalos*, etc., tends to become more emphasised.

Particularly important, as an evolutionary tendency, is the increase of subdivision in the leaf veins, and it is also important to note that apparently it appeared early in the history of growth-form evolution. The islands of assimilating tissue are relatively large in the more primitive, more tropical species. In the derivative type the ultimate reticulations are very small, and even the finer veinlets are often prominent and easily seen.

Experiments have been carried out at this centre (see Bews and Aitken, 1923) on the rates of drying out of various leaves, and it was found that, with a few exceptions, the finer the venation and the more fibre in the leaf, the slower the rate of drying out. Increase in the branching of the leaf veins appears, therefore, to be a xerophytic response to drier conditions.

It is not the only xerophilous evolutionary tendency shown by this class of growth forms. Various forms and degrees of pubescence are also shown, especially by the under surfaces of the leaves of certain hygrophilous species, e.g. *Antidesma*, *Croton* spp., etc.

While leaf characters are, on the whole, fairly easily investigated, there are other features distinctive of hygrophilous species which are more obscure. Large-leaved species with wide leaf-reticulations occur in the next class of mesophytic but not hygrophilous trees. There are even some rather xerophytic trees of open tree veld with larger leaves than some of the hygrophilous types. Water requirements are to be correlated with many anatomical and morphological features besides those of the leaves. The characters of the conducting elements, their distribution through the stem and their water-conducting capacity, etc., are all of importance, and here observation must be based on experiment.

The root systems of trees are also not so easily investigated,

but are clearly of the utmost importance. Many hygrophilous species have deep and wide-spreading roots, but our information on this point is scanty; and it is impossible to say what the evolutionary tendencies have been, for many xerophytes are known also to have deep and wide-spreading roots.

General evolutionary tendencies are best arrived at by comparing percentages or averages. If a high percentage of the species belonging to a certain class have a feature (such as large, simple, leathery leaves) in common, that feature may be taken as characteristic of the class. Exceptional cases must depend on other features, though it may not always be easy to say what they are. For the hygrophilous forest species of South Africa there is general agreement in the leaf characters mentioned above, and the number of exceptions is remarkably small. Detailed statistics will be considered later.

Mesophytic Forest and Scrub Types.—This is a very large and more heterogeneous class which occupies the various mesophytic habitats (the forest climatic areas) of the eastern side of South Africa. As explained already, these areas are the slopes which face the rain and mist-bearing winds from the south-east. As far as growth forms are concerned, the dominant and subdominant or associated trees which appear in the climax stages of the plant succession are to be considered more primitive and nearer to the tropical ancestral forms than the light-demanding more xerophytic smaller trees and shrubs which appear in the earlier stages of succession. As succession advances, the vegetation becomes more and more tropical in all types of plant community in subtropical areas. This was first noted as a general principle of plant succession in the detailed study of the coast-belt vegetation of Natal (Bews, 1920), where it is very clearly seen. From our present standpoint the principle is of considerable importance, since it enables us to arrange the mesophytic trees and shrubs in somewhat of a natural evolutionary sequence. It is the reverse of the sequence according to plant succession, and it is interesting that derivative species should be required to prepare the way in the plant succession for the development and spread of the more ancient, more primitive types of growth form. This subject will be referred to again later when the Karroo vegetation is dealt with (see Chapter IX).

The species of *Podocarpus*, which are often dominant in South African high forest, being gymnosperms are in a class by themselves. The three forest species, according to the latest

decisions by Stapf regarding nomenclature, are *P. latifolia* (= *P. thunbergii*), *P. falcata* (= *P. elongata*), and *P. henkelii* (= *P. falcata*). *P. elongata* is a Cape shrub. The names we have formerly given the different species (those in parentheses) seem to have been very wrongly applied. *P. latifolia* and

FIG. 7.—*Olea laurifolia* LAM.

½ nat. size. Sub-dominant tree in many mesophytic forests.

P. falcata are widespread over the whole eastern side. *P. henkelii* is the Drakensberg and Natal species with large distinctly falcate leaves (which *P. falcata* does not possess) and is the most mesophytic of the three; but, though dominant and sometimes forming almost pure stands in the forests where it occurs, is of the most distinctly local distribution, not being found north of the Mont aux Sources or south of East Griqualand. It descends through Natal to near Pietermaritzburg.

Among the Dicotyledonous forest trees, the single-boled sparingly branched, large or medium sized and flat-leaved, simple-leaved non-xerophytic species come nearest to the tropical type and may be considered most primitive in this sub-class of growth forms. In the moister spots the hygrophilous species already dealt with occur and there is no clear line of demarcation between hygrophilous and mesophytic.

The majority of the South African timber trees are included here as well as others of less economic importance. The following are representative examples: *Scolopia mundii* (Red Pear), *Scolopia zeyheri* (Thorn Pear), *Kiggelaria africana* (Wild Peach or Natal Mahogany), *Trimeria grandifolia* (Wild Mulberry), *Trimeria trinervis, Apodytes dimidiata* (White Pear), *Pittosporum viridiflorum, Garcinia gerrardi, Cola natalensis* (Umtenenenda), *Erythroxylon monogynum, Nectaropetalum zuluense, Calodendron capense* (Cape Chestnut), *Ochna arborea* (Redwood or Cape Plane), *Allophylus monophyllus, Pleurostylia capensis* (Mountain Hard Pear), *Gymnosporia peduncularis* (Blackwood), *G. nemorosa, Elaeodendron croceum* (Saffronwood), *Protorhus longifolia, Pygeum africanum* (Bitter Almond), *Trichocladus crinitus, T. ellipticus, Homalium rufescens, Gerrardina foliosa, Casearia junodi, Combretum kraussii, C. salicifolium, Weihea madagascarensis, Dactylopetalum verticillatum, Eugenia cordata* (Waterboom or umDoni), *Eugenia gerrardi, E. owariensis, Olinia cymosa, Curtisia faginea* (Assegai), *Rapanea melanophleos* (Cape Beech), *Maesa lanceolata, M. rufescens, Chrysophyllum natalense, C. viridifolium, Mimusops obovata* (Red Milkwood), *Olea laurifolia* (Black Ironwood), *Olea foveolata* (Bastard Ironwood), *Gonioma kamassi, Strychnos henningsii* (Hard Pear), *Nuxia floribunda* (Wild Elder), *Nuxia congesta* (Bogwood), *Chilianthus arboreus* (Bastard Olive), *Clerodendron glabrum, Cryptocarya latifolia, C. woodii, C. myrtifolia, C. sutherlandi, C. wyliei, C. liebertiana, Ocotea bullata* (Stinkwood), *Celtis rhamnifolia* (Camdeboo Stinkwood), *C. franksae, Trema bracteolata* (Pigeonwood), *Chaetacme aristata* (umKoboti), *Ficus capensis, F. natalensis, F. capreaefolia, F. nekbudu, F. burtt-davyi, Bridelia micrantha, Drypetes arguta, Antidesma venosum, Croton sylvaticus, Phyllanthus amapondensis, Macaranga capensis, Spirostachys africanus, Sapium mannianum, Heywoodia lucens, Notobuxus natalensis, Buxus macowani* (Cape Box). The last mentioned often forms pure associations in the coast forests near East London.

All the above examples have simple leaves; species with com-

pound leaves, however, are not so rare among mesophytic as among the hygrophilous forest types. The following are representative species with divided leaves: *Albizzia fastigiata* (Flat crown) has the leaves bipinnate and deciduous, but it usually occurs in open forest, though it may be dominant in mesophytic or hygrophilous forest. In the same family (Leguminosae) are included *Millettia caffra* (Umzimbete), *Millettia sutherlandi*, *Erythrina caffra* (Kafir Boom), *Umtiza listeriana*, and *Pterocarpus angolensis*. Other compound leaved species of forest trees are *Ptaeroxylon utile* (Sneezewood), *Rhus laevigata* (Red Currant), *Clausena inaequalis*, *Cunonia capensis* (Red Alder or Red Els), *Platylophus trifoliatus* (White Alder), *Ekebergia meyeri*, *Fagara davyi* (Knobthorn), *Vepris lanceolata* (White Ironwood), *Trichilia emetica* (Natal Mahogany or Umkuhlu), *Heteromorpha arborescens* (um-Bangandhlala), *Harpephyllum caffrum* (Kafir Plum), *Cussonia* spp., *Kigelia pinnata*.

FIG. 8.—*Vepris lanceolata* A. Juss.

With the exception of *Albizzia* the leaflets in all these species are of sufficient size to compare with the whole leaves of the simple-leaved species, which they resemble. All the species mentioned so far are trees, but among them are included many

that show a considerable plasticity in their growth forms, and these often occur outside the forest or in scrub as much-branched shrubs. In some cases, too, their leaf characters vary considerably, *e.g.* in *Heteromorpha arborescens,* the leaves of which are sometimes simple, sometimes compound, or both types of leaf may occur on the same twig. The leaves of nearly all the species vary greatly in size. As a rule, the nearer the conditions are to the tropical, as on the coast-belt, the larger the leaves.

A somewhat irregular deciduous tendency is shown by a few species, e.g. *Celtis rhamnifolia, Ptaeroxylon utile, Rhus laevigata,*

FIG. 9.—*Trichilia emetica* VAHL.
¼ nat. size. A single compound leaf.

Rauwolfia natalensis, Croton sylvaticus, Erythrina caffra, Calodendron capense. The deciduous tendency is much more pronounced inland than it is on the coast-belt. It may also be regarded as a derivative character in the evolutionary history of tree growth forms. There is again a general increase of minor xerophytic characters, such as leaf coverings, leaf sclerenchyma, reduction in size of the leaves, etc., in the less tropical, more derivative types.

Thorn development is still very rare, being shown by only a few forest trees, e.g. *Scolopia zeyheri* (Thorn Pear), which, however, according to Sim (1907), is sometimes spineless altogether. Sometimes ' the spines are absent from the crown but abundant on the main trunk which then bristles with much branched spikes, 6 to 8 inches long ; these form very hard knots right into the wood and continue to grow with the tree.' *Fagara*

davyi (Knobthorn or Umnungu-mabele) has characteristic rounded knobs on the stem ending in spines. *Erythrina caffra* has the branches more or less prickly. *Chaetacme aristata* is variable in form as well as in degree of spinescence. A few other thorny species, e.g. *Gymnosporia* spp. and *Plectronia* spp., are not single-boled trees or are more commonly much branched and shrubby and are not included in the above list.

A thick bark is a feature of a number of South African forest trees. It has been explained as a reaction to constantly occurring grass fires, but this explanation is very doubtful. It is shown by *Apodytes dimidiata*, *Trichilia emetica*, *Albizzia fastigiata*, *Pygeum africanum*, *Cunonia capensis*, *Eugenia cordata*, *Cussonia spicata*, *C. umbellifera*, *Curtisia faginea*, *Rapanea melanophleos*, *Olea laurifolia*, *Olea foveolata*, *Sideroxylon inerme*, *Rauwolfia natalensis*, *Ocotea bullata*, as well as others that grow more in open tree-veld, altogether a mixed group, and if it has any evolutionary significance it is at present obscure.

A free development of coppice shoots often modifies the original growth form in quite a number of forest trees, giving the appearance of an abnormally large trunk, or the main stem may die and become replaced by a cluster of coppice shoots. Examples :—*Xymalos monospora*, *Ocotea bullata*, *Kiggelaria africana*, *Rhus laevigata*, *Millettia caffra*, *M. sutherlandi*, *Nuxia congesta*. There are many others that show this feature to a greater or less extent, and it is important because it enables any individual tree to hold its position even after the death of the main stem. It also leads to the formation of a denser canopy in the forest.

Transitional between the South African mesophytic and hygrophilous forest types and the forests of the tropics is the interesting Chirinda mountain forests in the Melsetter district of southern Rhodesia, first described by Swynnerton, who collected extensively in this area. Henkel (1920) describes the component species as growing up to 200 feet high. *Khaya nyasica* is dominant, and other species include *Trichilia chirindensis*, *Lovoa swynnertonii*, *Maba mualala*, *Gardenia tigrina*, *Tannodia swynnertonii*, *Ehretia divaricata*, *Strychnos mitis*, *Schefflerodendron gazense*, *Pygeum africanum*, *Bosquiea phoberos*, *Croton sylvaticus*, *Ficus capensis*, *Myrianthus arboreus*, *Macaranga mellifera*, *Celtis dioica*, *Widdringtonia whytei*. The area covered by forest of this type is, according to Henkel, extremely limited. Lower-growing evergreen forest of the eastern border of southern Rhodesia with trees up to 80 feet high, Henkel describes as

growing in patches along the whole range of mountains. The following are representative species: *Cussonia umbellifera, Eugenia cordata, Eugenia gerrardi, Curtisia faginea, Neumannia theaeformis, Faurea* spp., *Eugenia owariensis, Podocarpus*

FIG. 10.—*Curtisia faginea* AIT.
½ nat. size.

melanjianus, Conopharyngia stapfiana, Maesa lanceolata, Piptadenia buchanani, Ekebergia meyeri, Kiggelaria africana, Pittosporum viridiflorum, Teclea swynnertonii, Teclea natalensis Rauwolfia natalensis, Bridelia atroviridis, Chrysophyllum natalense, Albizzia spp. This type is much more distinctly South African, but contains a fair proportion of species that do not extend further south.

The Evolution of the Shrub Form.—By far the most important evolutionary tendency in woody plant growth forms has been a general increase in branching. This has been accompanied by a general decrease in height, an increase in light requirements, and usually an increase in xerophytism. The final result is the replacement of the single-boled tree form by the many-stemmed shrub form, and the type of plant community is scrub rather than forest. Mesophytic scrub is usually marginal to forest and represents an earlier stage in the plant succession. The seeds of the taller forest trees germinate in the shade of the scrub, the seedlings grow up, and as they begin to overtop the light-demanding shrubby species they kill the latter by shading them. Only the mesophytic forest margin shrubby species will be dealt with in the present chapter. The more numerous tree-veld and xerophytic scrub species that are also derivative will be considered separately. While forest trees are found in twos and threes scattered through a large number of families, there are larger whole genera of shrubby forms and in some cases almost entire families. This in itself may be taken as an additional argument in favour of considering the shrubby type derivative. Phylogenetically, too, a higher percentage of mesophytic scrub species belong to highly evolved floral families among the Sympetalae.

The Rubiaceae include *Burchellia capensis*, *Tarenna pavettoides*, *Randia* (3 or 4 species), *Gardenia* (8 or 9 species), *Oxyanthus* (3 species), *Tricalysia* (4 species), *Alberta magna*, *Plectronia* (8 or 9 species), *Vangueria* (2 or 3 species), *Pavetta* (9 species), and *Psychotria capensis*, altogether over 40 species, though some of them, with others not included in the enumeration, are more characteristic of tree-veld and xerophytic scrub. The Rubiaceae show advance not only in their flower structure but also in their opposite leaves with interpetiolar stipules, an example of a purely vegetative character that has an accepted phylogenetic value. The ancestor or ancestors of the whole family must have had opposite stipulate leaves.

The Loganiaceae are not so highly evolved floristically, having the ovary superior, but the vegetative form and characters are similar with the leaves opposite and the interpetiolar stipules often reduced to a line or ridge. *Chilianthus* (2 species), *Buddleia* (3 species), and *Strychnos gerrardi* are forest margin or scrub types. *Buddleia salviaefolia* is one of the most abundant and widespread. Among the Ebenaceae various species of *Royena* and *Euclea* occur, but they are more characteristic of

xerophytic scrub. Species of *Solanum* are fairly common, and among the Scrophulariaceae, *Halleria lucida, H. ovata,* and *Anastrabe integerrima.* Belonging to the Acanthaceae are *Mackaya bella, Ruttya ovata, Adhatoda andromeda, A. duvernoia,* and *A. natalensis* with a host of suffrutices and herbs as undergrowth. In the Sapotaceae *Sideroxylon inerme* (White Milkwood) grows to tree size but is usually branched from the base, *Mimusops caffra* (Red Milkwood) is often dominant on the sand-dune (psammophilous) bush of the coast. *Maba natalensis* (Ebenaceae) is another characteristic coast species which grows to tree size. Among the Compositae there are five or six species of *Brachylaena,* of which *B. discolor* and *B. elliptica* are the commonest. Both are small trees. The Apocynaceae include *Carissa grandiflora, C. wylei, C. arduina,* and *Wrightia natalensis.* All the species mentioned so far are sympetalous. Among the Archichlamydeae certain families are well represented. The Euphorbiaceae have several species each of *Cluytia, Acalypha, Phyllanthus,* and *Sapium simii, Sapium reticulatum, Fluggea microcarpa,* and *Drypetes natalensis.*

FIG. 11.—*Mimusops caffra* E. M. ½ nat. size. Dominant tree in coast sand-dune bush.

The Leguminosae include *Baphia racemosa, Virgilia capensis* (Keurboom), an important pioneer, *Calpurnia sylvatica, Umtiza listeriana, Schotia latifolia, Cassia* spp., *Bauhinia natalensis, B. tomentosa,* and *B. bowkeri.*

Other genera and species are scattered through various

families, e.g. *Anona senegalensis, Maerua* spp., *Trichocladus crinitus, T. ellipticus, Gerrardina foliosa, Leucosidea sericea, Polygala* spp., *Rhus* (one or two species only, the majority being found away from forest), *Gymnosporia* spp., *Elaeodendron* spp., *Allophylus* spp., *Rhamnus prinoides, Grewia* spp., *Sparmannia palmata, Hibiscus* spp., *Rawsonia lucida, Doryalis* spp., *Peddiea africana, Combretum* spp., *Eugenia* spp.

All the shrubby species of the forest margin may be considered transitional to the tree-veld and scrub, which will be dealt with in the next chapter. They are nearly all capable of growing away from the forest altogether, and some of them will be referred to again. It is chiefly, however, in their increased branching that the forest margin species differ from the trees of the forest, and the true tree-veld and xerophytic scrub species tend to differ much more. Forest margin shrubs have much the same types of leaves as the taller trees, though the leaves are somewhat smaller on an average and show other minor increases of xerophytism. Thorn development is still rare. *Plectronia* spp., *Carissa* spp., and a few others show it. Compound leaves are proportionately not more common than among the tree forms. Taking the forest trees and shrubs together not more than 20 per cent. show leaf division, not more than 7 per cent. show thorn development, and at least 30 per cent. have leaves on an average over three inches long (not including the compound-leaved species). Statistics of this kind are very useful for purposes of comparison with more derivative types. It is only by dealing with fairly large numbers that general evolutionary tendencies can be established.

CHAPTER V

TREE-VELD AND XEROPHYTIC SCRUB TYPES

The main types of plant community to which the present class of trees and shrubs belong were named in our introductory chapter. The tree-veld of Rhodesia, the Kalahari and all the northern parts of South Africa is closely allied to the more xerophytic vegetation of the tropical regions. The thorn-veld of the eastern dry river-valleys and of the central and western areas is dominated chiefly by Acacias and is clearly another derivative type with tropical affinities. The sand-veld areas of Zululand as well as the Southern Kalahari are varieties of tropical tree-veld. Palm-veld (with *Hyphaene*) is simply an outlier in South Africa from the north. Succulent and thorny scrub, rocky hillside scrub of various kinds, are, on the whole, more characteristically South African. Protea-veld is a type by itself, allied to the mountain and south-western vegetation.

It was stated in Chapter III that the origin of many of the derivative types of growth form should be looked for within the areas of the tropics. This is particularly true regarding many of the dominant species. They do not connect clearly with the South African mesophytic forest species, which, it should be remembered, are themselves largely derivative from tropical forest types.

At the same time, in South African tree-veld and xerophytic scrub there are large numbers of species belonging to genera which also have representatives in high forest, and sometimes the history of the evolution of their growth forms is very clear. It may again be well to repeat, however, that linear series can never be made very long. If it were possible to arrange all the South African trees and shrubs in groups, such as (A) hygrophilous trees, (B) mesophytic trees, (C) mesophytic shrubs, (D) xerophytic thorny species, (E) succulent types, and so on, and to say that A,B,C,D,E represented a definite evolutionary sequence in which A gave rise to B, B to C, C to D, and D to E, this would

simplify matters exceedingly. Unfortunately it would also lead to very grave errors. Just as in systematic botany, based on floral characters, plants are grouped into families which have certain relationships to other families, so also growth forms may be arranged in natural groups which have evolutionary connections with other groups. Further, just as a family may have flowers that are primitive in some features but show high evolutionary advance in others, so growth-form classes may, in some respects, be ancient, in others very recent.

It is only after long and careful investigation that we can hope to be able to say what are the 'natural' groups of growth forms; but, at the same time, as our knowledge increases there will be greater certainty as to which growth-form characters are primitive and which are derivative and recent. Warming was right when he described the subject as 'very difficult yet very alluring.'

The classification we have adopted is, to a large extent, a habitat classification. This is inevitable, since growth form and habitat are closely connected. Plants are, on the whole, everyone will admit, adapted to their different environments. In a great continent like Africa the climatic habitats are of most importance, yet their effect, as we have seen, is sometimes not the dominating factor. This is particularly the case when there is excess of water in the soil. Other edaphic factors play a part in some varieties of tree-veld. The presence of Acacias in many cases is due to lime in the soil, most South African soils being very poor in lime.

The trees in the sand-veld areas are possibly modified also by the sandy nature of the soil, at least as far as their root systems are concerned.

Along the stream and river banks, and in marshy places away from the forest climatic areas, trees and shrubs are found which are different from the hygrophilous forest species already dealt with, though these also tend to spread into the drier areas in such situations.

Hygrophilous species of drier areas do show the effects of the climate in having smaller more xerophytic leaves and in being as a rule more branched, etc., and to that extent may be considered derivative, yet among them are included some undoubtedly very ancient types. Fossil evidence makes that certain. Other hygrophilous tree-veld and scrub species are more clearly to be connected with species of South African mesophytic forest. Apart, however, from species which also

occur in forest the numbers altogether are small. *Salix capensis* and *Salix woodii* with other species of Willow, recently described by Burtt-Davy (1922), represent one ancient type of growth form, though not necessarily of species. *Myrica conifera* and other species of *Myrica* are usually but not always hygrophilous. They occur also on sand dunes near the sea. This genus is the only representative of the Myricales, a primitive order. *Myrica quercifolia* and *Myrica cordifolia* are the sand-dune species. *Combretum erythrophyllum* is common along the Orange river and is recorded for the eastern side as well, though Sim throws doubt on the records. There are other species of *Combretum* which are sufficiently plastic to occur in different climatic areas provided they are near water, e.g. *Combretum salicifolium*, *C. kraussii*, *C. glutinosum*. *C. bracteosum* occurs on the Natal coast-belt and is also hygrophilous.

The genus *Royena* has *R. pallens* and *R. pubescens*, common along rivers and streams in the drier parts. *Rhus viminalis* and *R. lancea* are common along the Karroo river-beds, and several other species of *Rhus* are frequent in hygrophilous habitats over the eastern side. *Zizyphus mucronata*, though it occurs away from streams, prefers deep soil near water. *Acacia caffra* is a rather hygrophilous species of thorn tree, and there are others, e.g. *A. albida*, *A. nigrescens*.

In the more mesophytic climatic areas the list of stream-bank scrub species can be considerably extended. *Melianthus* spp., *Bowkeria* spp. (e.g. *Bowkeria triphylla*), *Gnidia ovalifolia*, *Ochna atropurpurea*, *Cliffortia strobilifera*, and *Psoralea pinnata* are representative examples, but there is a tendency, as already mentioned, for the spread of many of the mesophytic scrub and forest margin species along the streams and rivers into the drier climatic areas.

The total area covered by tree-veld and xerophytic scrub is vastly greater than the small area occupied by high forest in South Africa. The growth forms of the former are also much more diversified than those of the latter. Increased differentiation of form has, of course, been one of the main features of evolutionary progress. Before dealing with the growth forms further details are necessary regarding the composition and distribution of different types of tree-veld and scrub.

In Southern Rhodesia Henkel recognises three subtypes of deciduous savannah forest (as he prefers to name it), as follows :

A. *Baikiea plurijuga* subtype (Igusi). Representative

species: *Baikiea plurijuga*, *Copaifera coleosperma*, *Burkea africana*, *Pterocarpus erinaceus*, *Terminalia sericea*, *Ricinodendron rautanenii*, *Gleditschia africana*, *Combretum* spp., and numerous species of shrubs. This subtype is confined to the Kalahari sand-veld areas.

B. *Copaifera mopane* subtype (Mopane). Representative species: *Copaifera mopane*, *Lonchocarpus capassa*, *Acacia nigrescens*, *Bauhinia reticulata*, *Acacia* spp., *Combretum* spp., *Diospyros mespiliformis*, *Mimusops caffra*. This subtype, which often consists of pure *Copaifera mopane*, is representative of the tree flora of the hot valleys and depressions and is found scattered over wide areas.

C. *Brachystegia* subtype (Msassa). Representative species: *Brachystegia randii*, *B. bragei*, *B. filiformis*, *B. glaucescens*, *B. reticulata*, *Brachystegia* spp., *Uapaca kirkiana*, *Parinarium mabola*, *Afzelia cuanzensis*, *Protea abyssinica*, *P. mellifera*, *Protea* spp., *Faurea saligna*, *F. speciosa*, *Peltophorum africanum*, *Sclerocarya caffra*, *Bolusanthus speciosus*, *Pterocarpus sericeus*, *Pterocarpus erinaceus*, *Monotes* sp., *Lonchocarpus capassa*, *Zizyphus jujuba*, *Zizyphus mucronata*, *Ochna* sp., *Dombeya rotundifolia*, *Diplorrhyncus mossambicensis*, *Strychnos* spp., *Kirkia acuminata*, *Swartzia madagascariensis*, *Commiphora* spp., *Acacia* spp., *Combretum* spp., *Securidaca longipedunculata*, *Vitex* spp., *Diospyros mespiliformis*, *Erythrina tomentosa*, *Burkea africana*, *Rhus* spp., *Terminalia sericea* *T. brownei*, *Terminalia* spp., and in places the Baobab, *Adansonia digitata* with *Sterculia* sp. [The genus *Brachystegia* has recently been revised by Burtt-Davy and Hutchinson (1923), and some names have been added from their list to that of Henkel as given above.]

This subtype is by far the most extensive. Henkel estimates the area covered by it as over 64,000 square miles, principally in the more hilly parts of the country. Where edaphic conditions are favourable the type approaches high forest, notably on or at the foot of the numerous kopjes. In other cases, where the rainfall is low and the soil shallow, the type merges into scrub less than 10 feet high.

Henkel describes all the 'savannah forest' as of park-like general appearance. 'In the dry winter season, the trees with interspersed shrubs are leafless and in summer the foliage casts little shade. The trees, as a rule, are of small dimensions with large spreading crowns. The trees, according to locality and edaphic conditions, vary in height from 10 to 60 feet, and

from 6 to 36 inches diameter. The boles are, as a rule, short, from 6 to 30 feet with about 10 feet, as an average. The dominant trees belong to the Leguminosae order. The majority coppice freely, and, if not destroyed, or their growth retarded by recurring fires, soon re-establish forests over areas which have been clear-cut. The grass, which grows freely between the trees and shrubs during summer, does not form a close sward but is found in isolated tufts, leaving the soil more or less exposed. Where edaphic conditions are more favourable the trees close in and approximate close-type forests, but usually they are widely spaced, and, in some parts, where the soil is shallow, and the rainfall low, scrub-growth replaces trees. At the end of the dry season the trees and shrubs flush into leaf in an irregular manner.'

Burtt-Davy and Hutchinson (1923) note that the deciduous period of the Brachystegia forest is very brief—perhaps not more than two or three weeks of winter (at the end of July and beginning of August)—and further that the trees are scattered at intervals of 6 to 12, 20 or 30 feet, rarely more, sometimes less. Altogether they name or describe fifty-four species and give the general distribution of the Brachystegia forest as from Mafeking and the Magaliesberg northward to the great Congo basin. The leaves of all the species of *Brachystegia* are compound, paripinnate, with from sixty down to two pairs of opposite leaflets.

Henkel's work has added considerably to our knowledge of the composition and distribution of tree-veld in Southern Rhodesia. He estimates that it covers about 60 per cent. of the entire area. 'Standing on any eminence, the eye wearies with the immense stretches of bush-covered veld. In comparatively few parts are there any open stretches.' The types he describes extend far outside Rhodesia, but our knowledge of other subtropical regions remains somewhat meagre.

In Angola, on the western side, Pearson (1908–11) describes types in which *Copaifera mopane* is the dominant tree, and also refers to Acacia Veld and Baobab (*Adansonia*) Veld in the same region. Farther south in the South-Western Protectorate, according to Wagner (1916), 'East and south-east of the Otavi Range the plains have the character of gently undulating expanses of tree steppe, the aspect of which is rendered distinctly tropical by the presence of tall graceful palms (*Hyphaene ventricosa*). To the north and north-east

of the range they are, for the most part, covered with open forest, interspersed in the vicinity of Omuramba Ovambo with glades of delightful park-land.'

In Damaraland the tree-veld is essentially a thorn-veld. It is referred to by Pole Evans (1920) as the 'Damaraland Thorn-veld,' composed of *Acacia detinens* (Haakdoorn), *A. maras*, *A. heteracantha*, *A. dulcis*, *Dichrostachys nutans*, *Tarchonanthus camphoratus*, *Boscia pechuelii*, and *Combretum apiculatum*, with the succulents *Aloe rubrolutea*, *A. hereroensis*, and *Senecio longiflorus* on rocky hillsides.

In the dry river-valleys the trees are larger and consist chiefly of the Kameeldoorn (*Acacia giraffae*), *Acacia karroo*, *Zizyphus mucronata*, *Combretum primigenum*, and *Acacia hebeclada*. On the open sandy flats the Stinkbosch (*Boscia foetida*), *Lycium* spp., and *Catophractes alexandri* are common.

In Southern Damaraland *Acacia giraffae* is dominant with *A. karroo*, *A. detinens*, *A. stolonifera*, *A. hebeclada*, *Lycium* spp., *Boscia albitrunca*, and *B. transvaalensis*. In Namaqualand and Bushmanland the Kokerboom (*Aloe dichotoma*) is the most characteristic plant associated with other succulents and xerophytic shrubs, e.g. *Rhigozum trichotomum*, *Parkinsonia africana*, *Acacia detinens*, *Acacia* spp., *Boscia foetida*, *Catophractes alexandri*, and other smaller forms which will be dealt with later (see Chapter IX).

On the western side the increase of xerophytism from north to south is rapid and great. In the central and eastern regions the transition is more gradual.

The Bush-veld of the Transvaal is of a similar type to the Brachystegia tree-veld of Rhodesia. Representative species in it are: *Terminalia sericea*, *Combretum gueinzii*, *C. zeyheri*, *Burkea africana*, *Peltophorum africanum*, *Ficus* spp., *Faurea saligna*, *Cussonia* spp., *Boscia rehmanniana*, *Sclerocarya caffra*, *Odina discolor*, *Kirkia wilmsii*, *Acacia* spp. (numerous). Increasing xerophytism and a more distinct South African character are shown by the presence of Aloes and Euphorbias, e.g. *Aloe marlothii*, *A. wickensii*, *A. pienaarii*, *A. globuligemma*, *A. greatheadii*, *A. davyana*, *A. castanea*, *A. transvaalensis*, *Euphorbia ingens*, *E. cooperi*, and *E. tirucalli*, together with species of *Mesembrianthemum*, *Kalanchoe*, *Stapelia*, *Anacampseros*, etc., in the undergrowth on dry rocky hillsides.

The western and southern Transvaal, Griqualand West, Bechuanaland and the southern Kalahari, and the Northern Free State is all either open grassy country without trees, or where

tree-veld occurs it is usually thorn-veld. *Acacia giraffae* (the Camel-thorn), *A. detinens* (Haakdoorn), *A. karroo*, *A. stolonifera*, *Olea verrucosa*, *Tarchonanthus camphoratus* (Vaalbosch), *Boscia* spp., *Royena* spp., and the stream-bank types already described are most representative. Pole Evans (1920) describes scrub varying from 3 to 10 feet in height on the Asbestos Hills, composed of *Lebeckia macrantha*, *Tarchonanthus camphoratus*, *Rhus tridactyla*, *Olea verrucosa*, *Acacia detinens*, *A. stolonifera*, *Zizyphus mucronata*, *Nymania capensis*, and *Rhigozum* spp.

Fig. 12.—*Acacia benthami* Rochbr.
Much reduced. Dominant tree in much of the thorn-veld of Natal.
Illustrates the umbrella form.

Outside the eastern escarpment there are sharper contrasts, mesophytic forest alternating with thorn-veld, and succulent scrub, etc., in the river valleys, xerophytic scrub on the hillsides, and psammophilous bush on the coast sand dunes.

The term 'Thorn-Veld' is applied to tree-veld in which thorny species of Acacia are more or less dominant. The detailed plant succession in it was analysed in the Pietermaritzburg neighbourhood (Bews, 1917), and has been referred to in the earlier chapters. In the clumps which are often formed around the pioneer trees a great variety of more mesophytic species are found, including many already described as belonging to mesophytic forest.

Thorn-veld gradually passes into Thorny and Succulent Scrub in which numerous species of Aloe and various tree

Euphorbias, *Portulacaria afra*, etc., are dominant, mixed with a sprinkling of Acacias and a large variety of other xerophytic

FIG. 13.—*Smodingium argutum* SOND.
½ nat. size.

species. Representative species for the Fish river scrub have already been given (see Chapter III, p. 33).

The various types of thorn-veld, rocky hillside scrub, succulent scrub, and coast sand-dune scrub species are more distinctly South African, and a fuller enumeration is desirable.

As in the case of mesophytic forest, subordinate types of growth form, such as climbing plants, are omitted, since these will be dealt with separately later. The following are representative species arranged according to the families, and these, more or less roughly, in order of importance.

Leguminosae: *Acacia karroo, A. benthami, A. giraffae, A. detinens, A. hirtella, A. natalitia, A. litakunensis, A. lasiopetala, A. hebeclada, A. stolonifera, A. heteracantha, A. woodii, A. albida, A. xanthophloea, Acacia* spp., *Dichrostachys nutans, Schotia brachypetala, S. latifolia, S. speciosa, Erythrina tomentosa, E. caffra, E. humiana.*

Celastraceae: *Gymnosporia albata, G. acuminata, G. angularis, G. buxifolia, G. polyacantha, G. rehmanni, G. undata, G. woodii, G. rudatisii, G. concinna, G. capitata, G. maritima* (on sand dunes), *Pterocelastrus variabilis, Putterlickia verrucosa, P. pyracantha, Elaeodendron capense, E. aethiopicum, E. croceum, E. laurifolium, E. velutinum, E. kraussianum, E. sphaerophyllum.*

Anacardiaceae: *Heeria paniculosa, Heeria* spp., *Rhus lancea, R. viminalis, R. discolor, R. glaucescens, R. tomentosa, R. obovata, R. villosa, R. cuneata, R. excisa, R. crenata, R. grandidens, R. gueinzii, R. lucida, R. oblanceolata, R. parvifolia, R. puberula, R. tridentata, R. truncata, Rhus* spp., *Smodingium argutum* (see Fig. 13), *Sclerocarya caffra.*

Sapindaceae: *Allophylus erosus, A. monophyllus, A. decipiens, A. melanocarpus, Hippobromus alata, Pappea capensis.*

Melianthaceae: *Bersama* spp., *Melianthus* spp.

Euphorbiaceae: *Euphorbia grandicornis, E. cooperi, E. similis, E. ingens, E. triangularis, E. evansii, E. grandidens, E. tetragona, E. virosa, E. franchiana, E. coerulescens, E. ledienii, E. tirucalli, Drypetes arguta, Sapium* spp., *Cluytia* spp., *Croton rivularis, C. menyharti, C. gratissimus, C. zambesicus.*

Rhamnaceae: *Zizyphus mucronata, Rhamnus prinoides, R. zeyheri, Scutia commersoni, Phylica* spp.

Ebenaceae: *Royena lucida, R. cordata, R. scabrida, R. wilmsii, R. villosa, R. hirsuta, R. pallens, R. nitens, R. simii, R. glandulosa, Euclea lanceolata, E. ovata, E. natalensis, E. macrophylla, E. daphnoides, E. undulata.*

Oleaceae: *Jasminum* spp. (often climbing), *Olea verrucosa, O. mackenii, O. enervis.*

Rubiaceae: *Plectronia spinosa, P. ventosa, P. ciliata, P. gueinzii, P. pauciflora, P. mundii, Vangueria infausta, V. lasiantha, V. venosa, V. latifolia, Pavetta caffra, P. lanceolata,*

P. obovata, P. gerrardi, P. natalensis, Tricalysia lanceolata, Gardenia globosa, Randia rudis, R. dumetorum.

Sapotaceae : *Sideroxylon inerme, Mimusops obovata, M. oleifolia, M. dispar, M. concolor, M. caffra* (dominant in sand-dune scrub).

Loganiaceae : *Nuxia congesta, N. dentata, Buddleia salviae-*

FIG. 14.—*Euphorbia ingens* E. M.

Much reduced. Common and widespread in eastern dry river-valleys.

folia, Strychnos spinosa, Chilianthus arboreus, C. corrugatus, C. dysophyllus.

Apocynaceae : *Carissa arduina.*

Borraginaceae : *Ehretia hottentotica, Cordia caffra.*

Combretaceae : *Combretum* spp., *Terminalia sericea.*

Burseraceae : *Commiphora harveyi, C. caryaefolia.*

Ochnaceae : *Ochna* spp.

Rutaceae : *Fagara capensis, Clausena inaequalis, Vepris lanceolata.*

Tiliaceae: *Grewia caffra, G. lasiocarpa, G. hispida, G. flava, G. occidentalis.*

Sterculiaceae: *Dombeya cymosa, D. burgessiae, D. dregeana, D. natalensis, D. rotundifolia.*

Capparidaceae: *Maerua angolensis, M. rosmarinoides, M. nervosa, M. triphylla, M. woodii, M. racemulosa, Capparis tomentosa, C. woodii, C. calvescens, C. zeyheri, C. solanoides, C. rudatisii, C. gueinzii, C. albitrunca.*

Fig. 15.—*Myrsine africana* L. ½ nat. size. Common pioneer shrub.

Flacourtiaceae: *Oncoba spinosa, Scolopia zeyheri, Doryalis rhamnoides, D. tristis, D. caffra, D. celastroides, D. lucida, Homalium rufescens.*

Meliaceae: *Ptaeroxylon utile, Turraea floribunda, T. obtusifolia, Ekebergia capensis, Trichilia* spp.

Erythroxylaceae: *Erythroxylon monogynum.*

Portulacaceae: *Portulacaria afra.*

Rosaceae: *Cliffortia strobilifera.*

Umbelliferae: *Heteromorpha arborescens.*

Araliaceae: *Cussonia spicata, C. paniculata, C. umbellifera, Cussonia* spp.

Compositae: *Vernonia corymbosa, Tarchonanthus camphoratus, Brachylaena discolor, B. elliptica, Osteospermum moniliferum.*

Myrsinaceae: *Myrsine africana, Maesa rufescens.*

Solanaceae: *Solanum* spp., *Lycium* spp.

Scrophulariaceae: *Bowkeria* spp.

Bignoniaceae: *Rhigozum trichotomum.*

Verbenaceae: *Vitex mooiensis, V. harveyana, V. geminata, V. obovata, V. rehmanni, V. reflexa, V. zeyheri, V. wilmsii.*

Proteaceae: *Faurea saligna, Protea* spp.

Thymelaeaceae: *Dais cotinifolia, Peddiea africana, Lasiosiphon* spp.

Santalaceae: *Osyris abyssinica, Osyridocarpus natalensis.*

FIG. 16.—*Buddleia salviaefolia* LAM.
$\frac{1}{2}$ nat. size.

Among the Monocotyledons are the palms *Phœnix reclinata* and *Hyphaene crinita*, the latter forming Ilala Palm Veld in sandy soil along the coasts of Natal and Zululand. *Strelitzia augusta*, the wild banana, is common in coast scrub and tree-veld. In the Liliaceae the genus Aloe has numerous species very common on dry, hot rocky hillsides or in dry valley scrub.

Among the most important are: *Aloe marlothii, A. bainesii, A. ferox, A. arborescens, A. cooperi, A. nitens, A. candelabrum, A. thraskii* (on coast sand dunes), *Aloe transvaalensis, A. wickensii, A. pienaarii, A. globuligemma, A. greatheadii, A. davyana, A. castanea, A. pretoriensis, A. grandidentata,* and *Aloe dichotoma* (in the west). The cycad *Encephalartos altensteinii* is common in some of the valley scrub, and the tree fern *Cyathea dregei* is widespread, growing often out of old antbear holes.

Fig. 17.—*Phoenix reclinata* Jacq.
Much reduced. Common palm of Natal coast-belt.

The above list has been made a fairly detailed one (though it is by no means to be considered exhaustive) partly for convenience of reference, but chiefly to give a correct impression of the great variety of forms belonging to various types of tree-veld and scrub in South Africa. The growth forms and their evolutionary tendencies will now be considered.

The Monocotyledonous trees and shrubs with Cycads and Tree Ferns are in a group by themselves, totally different from the Dicotyledons, and may therefore be dealt with first. Warming (1909) places them, except the Aloes, in a class of 'Tuft-trees' (Drude's 'Schopfbaume,' 1896) which he defines as 'Shoots with short internodes; leaves densely set on the end of the shoot, large and few; buds usually naked. Stems unbranched or with only a few thick branches, none of which are thrown off,' and he divides them into three subtypes.

1. Trunk unbranched. Leaves large and divided. Tree

Ferns, Palms, and Cycads. (This includes our South African *Phoenix reclinata*, *Hyphaene* spp., *Raphia vinifera*, *Cyathea dregei*, and various species of *Encephalartos*.

2. Trunk sometimes sparsely branched, showing secondary thickening. Leaves undivided. *Dracaena*. The only native South African species, *Dracaena hookeriana*, grows in shade.

3. Strelitzia form.

Warming places the Aloes among Rosette plants, though some of them might equally well be considered tuft trees. They are a group of considerable importance in South Africa. Seventy species are described in the 'Flora Capensis,' but this number has been greatly added to since that work was published by Dr. Pole Evans and others. Visitors to South Africa are able to see a magnificent display of them in cultivation around the Union Buildings, Pretoria.

If the Aloes are included, the number of succulent species in South African succulent scrub is greatly increased, but for comparative purposes it is difficult to include any Monocotyledons in any of the growth-form groups of trees and shrubs since they are phylogenetically so distinct.

Among the Dicotyledons the various trees and shrubs of tree-veld and scrub show various salient characters.

1. There is a general reduction in size which increases more or less in direct proportion to increase of aridity. There is always a certain plasticity in this respect among the taller trees, but in others the low-growing habit has become fixed.

2. Decrease in size is usually associated with increased branching, producing a shrub-form instead of a tree-form. In tree-veld, however, the branching often does not take place from near the ground but from a height of a few feet. A short main trunk then carries a widespread umbrella-shaped canopy of spreading branches, a common type among Acacias and in *Albizzia*, etc. In the more tropical tree-veld (e.g. *Brachystegia* spp.) branching is not so prominent (see Fig. 12).

With continued decrease in size the shrub form passes into the suffrutescent form, and derivative types have become adapted to a subordinate rôle as associated plants in grass-veld areas. They are still woody, but the main branched woody stem is often entirely underground, and more or less herbaceous annual shoots are produced above ground. Burtt-Davy in a recent paper (1922) has dealt with examples of this type in the genera *Acacia*, *Clerodendron*, *Elephantorhiza*, *Erythrina*, *Eugenia*, *Menodora*, *Myrica*, *Parinarium*, and *Zizyphus*.

3. There is a general decrease in size of the leaves as compared with those of high forest species, though there are several notable exceptions to this rule. When averages of all the species are taken, however, the decrease is seen to be very well marked. Statistical comparisons will be made later.

FIG. 18.—*Cussonia paniculata* E. & Z.
Much reduced.

4. Compound leaves are much more common in tree-veld and scrub types than in forest types. The large genera *Acacia*, *Rhus*, and *Brachystegia* alone contain about a hundred species between them, or if we take the continent as a whole about 240 species. Their size in itself shows how successful the divided-leaved type has been under conditions of greater aridity, more intense illumination, etc. The whole of the

vast savannah forests of Rhodesia and South Central Africa are dominated by compound-leaved Leguminosae, and the family in South African tree-veld and scrub includes *Acacia, Erythrina, Schotia, Virgilia*, and *Albizzia*. Other compound-leaved genera are *Maerua, Vepris, Teclea, Fagara, Clausena, Allophylus, Smodingium, Harpephyllum, Ekebergia, Ptaeroxylon, Commiphora, Cussonia, Heteromorpha, Vitex*, and *Jasminum*. There are certainly not less than 40 per cent. of tree-veld and scrub species with divided leaves, or at least twice as many as in close forest, even if we include in the latter the marginal scrub species.

In hygrophilous forest, which comes nearest to the ancient tropical type, not more than 5 or 6 per cent. of the species have compound leaves.

5. An irregular deciduous tendency was noted for a few trees in mesophytic forest. In tree-veld the tendency is much more pronounced. The whole of the savannah forest of Rhodesia is described by Henkel as deciduous, even though the leafless period may be a short one. In South Africa most of the thorn-veld species are to be found bare of leaves for short periods, and some are regularly deciduous, e.g. *Erythrina* spp., *Commiphora* spp., *Bersama* spp., *Brachystegia* spp., and others.

6. Spinosity. The production of thorns in response to increasing aridity is a feature of a large number of tree-veld (especially thorn-veld) and xerophytic scrub species. Practically all the South African species of Acacia are thorny, often extremely so in the drier central and western areas, where they appear as one mass of thorns with hardly a leaf to be seen. In addition, the following are armed: *Zizyphus mucronata, Doryalis caffra, D. celastroides, D. rhamnoides, Lycium* spp., *Solanum* spp., *Capparis* spp., *Erythrococca* spp., *Chaetacme aristata, Putterlickia* spp., *Gymnosporia* (at least a dozen species), *Oncoba spinosa, Scolopia zeyheri, Ximenia caffra, Scutia commersoni, Azima tetracantha, Carissa* spp., *Gardenia neuberia, Plectronia* spp., *Strychnos* spp., *Royena pentandra, Erythrina* spp., *Dalbergia armata, Fagara capensis, Euphorbia* spp., and several others.

Altogether about 25 to 30 per cent. are more or less spiny. Thorns have been looked on as a protection against grazing herbivores, and there is little doubt that they do have the effect, though this probably had little to do with their production in the course of evolutionary history. They are found

in a few species which grow in close forest or in the case of one or two South American palms (*Astrocaryum* and *Bactris*), even in rain-forest. Some lianes climb by means of thorns or prickles. They only become common, however, in species which grow in the open in drier areas, and the drier the area the more they increase in abundance and size on the individual species. This is very well illustrated in the South African flora. In general the production of thorns may be looked upon as one of the visible results of the process of lignification which is characteristic of xerophytes. It is seen in leaf texture as well and appears to be intimately connected with water-holding capacity during periods of drought.

In many species vigorously developing branches, the so-called 'gourmand shoots' of the gardener, are often much more spiny than the rest of the plant. So also when thorny species are kept cut back as a hedge, thorn development is increased. The exact significance of this fact is rather obscure. Lothelier (1890–3) found that in the case of *Ulex europaeus* normally spiny branches, if kept in moist air or in feeble light, became leafy spineless shoots. Intense illumination as well as dry air he looks upon as favouring thorn development.

Whatever the explanation of the cause of thorn development there is little doubt that thorny species are derivative.

7. Succulence. Among Dicotyledonous trees and shrubs the great succulent genus of South Africa is *Euphorbia*. The chief species have been named in the list given above. All of them except *Euphorbia tirucalli* are spiny as well as succulent, and the type represents the most highly specialised example of tree growth form. Reduction in size, however, is here the tendency as elsewhere, and the great majority of the succulent species of Euphorbia are smaller forms. Among the tree-forms *Euphorbia ingens* is the most important of the Candelabra forms, followed by *E. grandidens*, *E. tetragona*, and *E. triangularis*, which extend further south. *E. tirucalli* is very abundant in the Tugela river-valley in Natal. *Portulacaria afra* (the Spekboom, see Fig. 1) is dominant or sub-dominant in much of the Fish river scrub and is common elsewhere. *Salsola aphylla* has small fleshy, closely imbricating leaves. It forms scrub on Karroo hillsides. *Adenium* (three species) and *Pachypodium* (four species) (Apocynaceae) are succulent shrubs, sometimes with much swollen trunks and fleshy branches. The former genus is unarmed, the latter armed with spines.

With general reduction of size the succulent scrub types

merge into the more numerous succulent dwarf shrubs and herbs of the Karroo and drier western regions, in which class it might be well to include them all except the tree Euphorbias and Portulacaria.

There can be no definite lines drawn between different classes of growth form any more than between many genera and families. It is indeed obviously much more difficult to do so in the former case than in the latter.

8. There is a general well-marked increase among thorn-veld and scrub species of minor xerophytic characters. These are almost too numerous to mention. Coverings of hairs of various kinds, coverings of scales, coverings of wax on the leaves, varnished leaves, sunk stomata, increased hardness of the leaves due to increased branching and thickening of the veins, schlerenchyma and stone cells (idioblasts) in the chlorenchyma, thick cuticle, ethereal oils (especially in the Rutaceae) all are common.

There is room for a great deal of very useful work in arranging, cataloguing and determining the relative frequency of these various devices in the xerophytic shrub flora of South Africa.

It will also be necessary ultimately to decide what value, if any, each character possesses in the evolutionary classification of growth forms.

9. In conclusion, it may again be pointed out that many of the genera in tree-veld and scrub are very large. *Acacia, Rhus, Brachystegia, Gymnosporia, Royena, Euclea, Euphorbia*, and several others are out of all comparison greater than any single genus among the mesophytic and hygrophilous trees and shrubs of South Africa. This is to be correlated partly with the much greater area covered by the xerophytic derivative types in South Africa. The South African species of genera in the high forest are more often simply outliers of large tropical genera, while the tree-veld and scrub genera are more distinctly South African or at least extra-tropical. At the same time, a fair proportion of mesophytic trees belong to genera that are small even in the continent as a whole. They may sometimes be of the nature of relict forms, or differentiation may simply be greater among the more ancient types. Some tropical-subtropical tree families in Africa consist of a large number of genera and a relatively small number of species; others have few genera and a large number of species. Further general comparisons of this kind will be dealt with in the next chapter.

CHAPTER VI

SUMMARY OF EVOLUTIONARY TENDENCIES IN SOUTH AFRICAN TREES AND SHRUBS. STATISTICAL COMPARISONS. SUBORDINATE TYPES.

Subordinate woodland types of growth form—Climbing plants, or lianes—Epiphytes—Parasites—Undergrowth.

By comparing the different types of growth form in the order in which they have been dealt with, we can now summarise some of the main evolutionary tendencies. It should be clearly realised, however, that caution is necessary in any particular case, and absolute certainty in the detailed application of the results in the present state of our knowledge is probably impossible. At the same time, the evidence, as we have seen, from ordinary phylogeny and all that we can trace of the past history of the continent and the present day, as well as past migrations of the flora, support our view that the hygrophilous and mesophytic tropical and subtropical trees are of the most ancient type, while the trees which colonise open grasslands, and finally the thorny and succulent scrub, are more recent.

Mangroves and other seashore types are in a class by themselves, and probably have not altered much with the lapse of time or given rise to other derivative types.

In inland forests the most primitive type of trees are the single-boled, simple-leaved, sparingly branched, tall-growing type. Their leaves are large, evergreen, as a rule rather leathery, smooth and glossy, without hairs or other coverings. The familiar Magnolia leaf may be taken as a fairly good example. See also the drawing of *Xymalos monospora* (Fig. 3), which is better, since it belongs to a more mesophytic species.

The Hygrophilous trees of moist climatic areas in South Africa are of a very uniform, primitive, growth-form type, but even among them marked variations in the amount of leaf-sclerenchyma and in the amount of branching in the veins

occur. The species with large islands of chlorenchyma in the leaves are more tropical; leaves with smaller reticulations tend to occur more often inland and are more derivative.

This evolutionary tendency requires further investigation, but it is very interesting, since it appears among the most primitive types. With increasing aridity the first and most obvious result is increased diversity of form. This is accompanied by a general reduction in size of the species, with a marked increased branching producing the shrub type. Slow continuous branching above a certain level (usually only a few feet) gives the spreading umbrella form. The change in form is further accompanied by general increase in xerophytism. There is a decrease in the average size of the leaves, an increase in leaf modifications adapted to resisting water loss, an increase in leaf division, and the deciduous tendency becomes more marked. There is a very prominent tendency to develop thorns.

The genus *Euphorbia* has developed succulence while retaining the tree form, but succulence is usually accompanied by a marked decrease in size to the dwarf shrub and herbaceous type found in the Karroo and among the Dicotyledonous trees and shrubs; therefore the percentage of succulents is not very high.

In Table I an attempt is made to give a statistical analysis of the subtropical trees and shrubs of South Africa. The Aloes and other Monocotyledons are not included, and only some of the main growth-form characters are dealt with, since our information regarding more detailed features is not yet sufficiently exact.

TABLE I

Dicotyledonous Subtropical South African Trees and Shrubs.

	Total.	Percentage.
Total number of species dealt with	800	100
Species with thorns or prickles	120	15
Unarmed species	680	85
Succulent species	24	3
Species with simple leaves over 3 inches long	160	20
Species with simple leaves 3–1 inches long	320	40
Species with simple leaves less than 1 inch long	70	9
Species with compound leaves	250	31
Species with opposite leaves	210	26
Species with alternate leaves	590	74

In drawing up the table over 700 species were card catalogued with full descriptions. An extra hundred was added because of the difficulty in drawing an exact line between the eastern shrubs and dwarf shrubs of the Karroo, and the borderline forms were apportioned between the different leaf classes. The south-western and mountain flora was not included. The table may be taken as accurate to within 1 or 2 per cent., which is more than is necessary for the purpose in view. By itself it illustrates to what extent the various evolutionary modifications already described have become established in the South African subtropical trees and shrubs. More information, however, can be obtained by using the percentages given as a 'normal spectrum' and comparing with it the different classes of growth forms which represent different stages of evolutionary progress as shown in Table II.

TABLE II

South African Subtropical Trees and Shrubs.

	Total Number dealt with.	Thorny.	Succulent.	Leaves Simple over 3 Inches.	Leaves Simple 3-1 Inches.	Leaves Simple under 1 Inch.	Leaves Compound.	
		%	%	%	%	%	%	
South Africa as a whole	800	15	3	20	40	9	31	Normal Spectrum
Hygrophilous types	60	2(?)	0	75	19	0	6	
Mesophytic forest types	150	7	0	32	47	3	18	
Tree-veld and scrub types	500	24	5	11	34	13	42	

The important information is to be obtained from this table not by comparing the percentages in each class separately but by noting the differences from the normal spectrum. The large percentages for large simple leaves in the hygrophilous class show the general uniformity. The better distribution of percentages for the tree-veld and scrub types shows the much greater diversity of growth form. The increase of thorn development, the establishment of the succulent form, and the general decrease in size of the leaves are also demonstrated. Most interesting of all is the marked increase in the percentage of compound-leaved species in tree-veld and scrub.

The hygrophilous and mesophytic trees and shrubs of South Africa are fairly evenly scattered through a number of important tropical woody families that are generally much better represented in Central Africa.

The South African representatives are not only comparately few in numbers but the average size of the genera is small. The statistics in Table III have been selected from Thonner's 'Flowering Plants of Africa' (1915).

Table III

Families of Tropical-subtropical Trees and Shrubs mainly Hygrophilous or Mesophytic.

	Africa as a whole.			Central Africa.			South Africa.		
	Gen.	Species.	Spec. Gen.	Gen.	Species.	Spec. Gen.	Gen.	Species.	Spec. Gen.
Anonaceae . .	26	230	8·8	25	200	8·0	5	8	1·6
Monimiaceae .	6	30	5·0	3	6	2·0	1	1	1·0
Pittosporaceae .	1	35	35·0	1	15	15·0	1	2	2·0
Erythroxylaceae .	2	40	20·0	...	...	...	1	4	4·0
Hippocrateaceae .	3	110	36·6	3	100	33·3	2	5	2·5
Icacinaceae . .	19	90	4·7	15	65	4·3	3	5	1·6
Sapindaceae .	47	200	4·2	29	120	4·1	8	15	1·8
Flacourtiaceae .	46	250	5·4	39	150	3·9	11	25	2·3
Lecythidaceae .	4	15	3·7	3	8	2·6	1	1	1·0
Rhizophoraceae .	10	45	4·5	8	30	3·8	4	5	1·2
Apocynaceae .	57	440	7·7	42	330	7·9	12	30	2·5

In these families, while in Africa as a whole, including the islands, there are 6·7 species to the genus, while Central Africa has an average of 6·1, in South Africa there is an average of only 2. Other families are more mixed, containing mesophytic as well as xerophytic forms, but the following may be selected as containing at least a fairly high proportion of tree-veld and scrub types. Table IV shows that in such families the genera in the tropics, or in Africa, as a whole, are not on an average much larger than in South Africa. It is true that several of the larger families contain a large number of herbaceous genera, but including these (as being also derivative) the comparative sizes of the genera are: Africa as a whole, 12·0; Central Africa, 8·6; South Africa, 9·7.

TABLE IV

	Africa as a whole.			Central Africa.			South Africa.		
	Gen.	Species.	Spec./Gen.	Gen.	Species.	Spec./Gen.	Gen.	Species.	Spec./Gen.
Leguminosae	253	3300	13·0	182	1650	9·1	88	1000	11·3
Rutaceae	30	310	10·3	17	80	4·6	17	210	12·3
Euphorbiaceae	117	1150	9·8	95	600	6·3	31	220	7·1
Anacardiaceae	26	240	9·2	16	130	8·1	9	95	10·5
Celastraceae	15	160	10·7	5	50	10·0	11	90	8·2
Rhamnaceae	18	140	7·2	14	25	1·8	8	90	11·2
Sapotaceae	16	140	8·7	12	110	9·1	3	15	5·0
Oleaceae	10	120	12·0	5	70	14·0	5	20	4·0
Loganiaceae	14	240	17·1	8	170	21·2	8	25	3·1
Combretaceae	12	330	27·5	10	280	28·0	4	25	6·2

These tables demonstrate sufficiently clearly what was stated at the end of the preceding chapter. The more typically mesophytic and hygrophilous families have genera, on an average, at least three times as well represented in the tropics as in South Africa; while the families that are more characteristic of tree-veld and xerophytic scub consist of genera that are, on the whole, as well represented in South Africa as in the tropics (and within the tropics they are found chiefly in the drier parts).

Subordinate Woodland Types of Growth Form.—The various woodland types of plant community are not composed wholly of trees and shrubs. There are various types of growth form (climbing plants, epiphytes, parasites, undershrubs, and herbs) which find a place in forest and scrub as associated plants. They are subordinate to and dependent on the presence of the dominant trees and shrubs, and in a very general way probably their migrations and evolutionary history run parallel to those of the trees and shrubs. Details, however, in this case are more uncertain. It is possible, though unlikely, that such subordinate types of angiospermous growth forms may have existed in pre-Cretaceous times in gymnospermous forests. They are widely scattered through the families of Angiosperms, and many of them are undoubtedly very ancient. The evidence on the whole, however, supports the common-sense view that the majority of the subordinate forms found in each of the present-day types of woodland

plant community were evolved after the establishment of each such type. Thus the undergrowth and climbing plants of tropical forest are, on the whole, younger than the dominant trees; the undergrowth of tree-veld, of xerophytic scrub and so on is, in each case, younger than the trees and shrubs on whose presence the undergrowth depends, and all types of subordinate growth form with increasing xerophytism become more and more recent.

All this, however, has little or no bearing on the actual origin of the subordinate types. They have not been evolved directly from the trees and shrubs among which they occur. Their growth forms are more ancient than the Angiosperms. Climbing ferns occur in South African forests at the present day. Epiphytes and herbs are, of course, as ancient as the earliest land plants.

Among primitive types of habitat which have persisted more or less unchanged since the rise of the Angiosperms there is a close connection between marshes and the moist marginal fringe of the forest.

Even at the present day the types of vegetation in these two habitats are closely similar. As we have seen, the evidence from phylogeny supports the view that, in such situations, many ancient types occur, and it is probable that the undergrowth of the forest originated near the forest margin or in marshes. Climbing plants have probably been derived from the light-demanding, much-branched, marginal species of trees and shrubs. The forest margin is by far the richest in genera and species. Only relatively few of the subordinate forms penetrate through the forest.

Just as increasing aridity has been the most important factor influencing the course of evolution among the trees and shrubs, so in the case of associated woodland plants there has been adaptation to increased shade. This has profoundly modified the growth forms and physiological processes. The presence of taller plants has been a factor which has modified and complicated the inorganic environment for all subordinate types, though even among the trees and shrubs themselves the same factor is not without significance. At the same time, the inorganic environment and particularly increasing dryness has also had an important effect on the subordinate woodland types as they have migrated into or been evolved in South Africa. Among the most recent, for instance, are various succulent climbers belonging to the Asclepiadaceae, and the undergrowth

of xerophytic scrub is allied to the associated plants of the grass-veld which, in turn, are allied to the plants of the Karroo. Grass-veld plants also probably originated in marshy places or around the forest margins, but have been influenced in their evolution chiefly by the increasing aridity. The undergrowth of the forest has become specialised in other directions, but is also probably mostly derivative. Since the habitat, however, is a more ancient one, some of the forms, *e.g.* the Peppers, Aroids, etc., may be very ancient. Different classes of growth form will now be considered separately.

1. Climbing Plants, or Lianes.—The term 'liane' was originally used only for woody climbers, but is now generally applied to the whole group. The climbing habit is obviously derivative, but it has risen again and again in widely different circles of affinity. Climbing ferns occur in the coast forests of Natal, e.g. *Lygodium scandens, Stenochlaena tenuifolia, Polypodium lycopodioides*. There is no reason why the climbing habit should not have arisen, therefore, very early in the evolutionary history of the Angiosperms.

The great majority of lianes belong to the tropics, though they are not rare in cold temperate countries as well. Schenck is quoted by Schimper (1903) as giving an estimate, which probably errs on the side of being too low, that over 90 per cent. of lianes are tropical. Climbing plants have usually been classified as simple scramblers, leaning for support on other plants, or twiners, or according to the particular organs that are modified to assist in climbing (stems, branches, leaves, roots, inflorescence axes). These three main classes probably do represent very roughly different stages in the evolutionary history of the growth form, but the modifications of the different organs have less significance.

In the South African flora climbing plants are scattered through a wide range of families, both Monocotyledonous and Dicotyledonous, as follows :

Nyctaginaceae : *Pisonia aculeata.*
Ranunculaceae : *Clematis* spp.
Menispermaceae : *Cissampelos* spp.
Anonaceae : *Uvaria caffra, Popowia caffra, Artabotrys monteiroae.*
Papaveraceae : *Corydalis* spp.
Cruciferae : *Heliophila scandens.*
Capparidaceae : *Capparis* spp., *Cadaba natalensis, C. juncea.*

Saxifragaceae : *Choristylis rhamnoides.*

Rosaceae : *Rubus* spp.

Connaraceae : *Cnestis natalensis.*

Leguminosae : *Dalbergia* spp., *Vigna* spp., *Canavalia* spp., *Dolichos* spp., *Teramnus labialis, Fagelia bituminosa, Entada* spp., *Acacia* spp.

Malpighiaceae : *Acridocarpus natalitius, Sphedamnocarpus* spp. (see Fig. 19).

Euphorbiaceae : *Dalechampia* spp., *Ctenomeria* spp., *Tragia* spp.

Hippocrateaceae : *Salacia* spp.

Icacinaceae : *Pyrenacantha scandens.*

Rhamnaceae : *Scutia commersoni.*

Vitaceae : *Rhoicissus* spp., *Cissus* spp.

Passifloraceae : *Tryphostemma sandersoni, Adenia* spp. (stragglers in grass-veld).

Achariaceae : *Ceratiosicyos eckloni.*

Combretaceae : *Quisqualis parviflora, Combretum bracteosum.*

Myrsinaceae : *Embelia ruminata.*

Plumbaginaceae : *Plumbago capensis.*

Oleaceae : *Jasminum* spp.

Apocynaceae : *Landolphia* spp., *Strophanthus* spp., *Oncinotis inandensis.*

Asclepiadaceae : *Cryptolepis* spp., *Stomatostemma monteiroae, Tacazzea* spp., *Chlorocodon whytei, Secamone* spp., *Astephanus* spp., *Microloma* spp., *Glossostephanus linearis, Pentarrhinum* spp., *Cynanchum* spp., *Sarcostemma viminale, Pergularia* spp., *Tylophora* spp., *Emplectanthus* spp., *Marsdenia floribunda, Telosma africana, Fockea* spp., *Gymnema sylvestris, Riocreuxia* spp., *Ceropegia* spp., including altogether about 90 species.

Convolvulaceae : *Ipomaea* spp., *Hewittea bicolor, Convolvulus* spp., *Evolvulus* spp.

Verbenaceae : *Lantana* spp.

Bignoniaceae : *Podranea ricasoliana* and sometimes *Tecomaria capensis.*

Acanthaceae : *Thunbergia* spp.

Cucurbitaceae : About a dozen genera and between 30 and 40 species, but many are stragglers in grass-veld.

Compositae : *Anisochaeta mikanioides, Mikania scandens, Senecio* spp. (sect. *scandentes*).

Gramineae : *Panicum* spp., *Pollinia nuda, Potamophila prehensilis, Olyra latifolia, Stipa dregeana.*

Flagellariaceae : *Flagellaria guineensis.*
Liliaceae : *Smilax kraussiana, Behnia reticulata, Asparagus*

FIG. 19.—*Sphedamnocarpus galphimiaefolius* A. Juss.
½ nat. size.

spp., *Gloriosa virescens, G. superba* (see Fig. 20), *Bowiea volubilis.*

Dioscoreaceae : *Dioscorea* spp.

Altogether there are over 300 species, or nearly 40 per cent. of the number of the tropical-subtropical trees and shrubs, but the numbers have been increased by including many herbaceous stragglers along the forest margins and in grass-veld and drier regions of the centre and west. The Asclepiadaceae alone include over 90 species. Among the larger genera are *Ceropegia, Ipomaea, Cissus, Asparagus*, and *Dioscorea*. Among the herbaceous climbers there is a distinct tendency to the production of the annual type, another indication of their derivative character.

FIG. 20.—*Gloriosa superba* L.
⅓ nat. size.

While a few climbers belong to relatively primitive families, such as Ranunculaceae (*Clematis*), Anonaceae, Menispermaceae, Capparidaceae, etc., the great majority belong to relatively highly developed phylogenetic groups—*e.g.* Asclepiadaceae, Cucurbitaceae, Convolvulaceae—indicating that no matter how early the climbing habit appeared the great majority of present-day climbers are relatively recent.

Probably the most ancient type of growth form is the woody liane of the tropical-subtropical forests. South African examples of this type include: *Dalbergia* spp., with woody ‘watchspring’ tendrils, *Cissus* spp., *Rhoicissus* spp., *Scutia commersoni* (*S. indica*), *Artabotrys monteiroae*, *Popowia caffra*, *Cnestis natalensis*, *Entada* spp., *Strophanthus* spp., *Landolphia*

spp., *Oncinotis inandensis*, *Podranea ricasoliana*, *Senecio* spp., *Behnia reticulata*. Of these *Scutia* and *Dalbergia armata* are thorny. Several are sufficiently plastic to illustrate in themselves the probable early evolutionary history of the climbing growth form. *Scutia commersoni*, for instance, often grows in open scrub as a shrub or even as a small tree, yet in tall forest it is one of the tallest of the woody lianes or 'monkey ropes,' overclimbing the highest trees and, according to Sim (1907), 'producing such a dense mass of foliage that it inevitably kills the tree it hangs upon.' Similarly *Dalbergia* spp., *Strophanthus* spp., *Jasminum* spp., and others often grow erect in the absence of support.

Outside the forest, along the forest margin in tree-veld or xerophytic scrub, with increasing aridity the same evolutionary tendencies are shown by climbing plants as by trees and shrubs, but these are carried farther, producing the herbaceous type and even the annual type. Underground storage is frequent, *e.g.* in *Dioscorea* spp., *Cissus* spp., and many Asclepiadaceae. There is much greater diversity in type. As in the case of the trees and shrubs, about 15 per cent. are thorny. Succulence is more in evidence than among trees and shrubs. Many Asclepiadaceae, *Cadaba juncea*, etc., show it. The majority of the South African Cucurbitaceae and Passifloraceae, and many of the Convolvulaceae, Asclepiadaceae, Vitaceae, and Leguminosae are stragglers in open spaces rather than climbers in the bush.

If true forest lianes alone were included, the numbers would be much reduced. In the tropical forests of central Africa climbing palms, e.g. *Calamus* (6 species), *Oncocalamus* (2 species), *Eremospatha* (5 species), *Ancistrophyllum* (1 species), and *Laccosperma* (2 species), climbing Aroids, e.g. *Rhektophyllum* (2 species), *Alocasiophyllum* (1 species), *Cercestis* (7 species), *Culcasia* (17 species, not all climbing), *Afroraphidophora* (2 species) occur, but none of these reach South Africa though both families are represented.

Such tropical woody genera of lianes as do reach South Africa are much impoverished in numbers. Thus *Dalbergia* has 65 species in tropical Africa, but only 2 reach South Africa; *Cnestis* has 30 African species, with *C. natalensis* as the only South African representative; *Landolphia* has 45 species, of which only 2 or 3 extend as far south as Zululand. The Menispermaceae, which are usually climbers, have 27 genera and 100 species in Africa, but only 6 genera and 15 species in South Africa. The South African forests have retained only a

vestige of the rich luxuriance of the tropical forests in lianes as in other subordinate types of growth form. The majority of South African climbing plants are more xerophytic—the 90 odd species of Asclepiadaceae help to swell the numbers—more herbaceous, more often stragglers outside the forest or prostrate creepers through the grass-veld, though these more properly should not be included here, and only a few of them, particularly the Cucurbitaceae and Passifloraceae, have been included.

2. Epiphytes.—In addition to bearded lichens (*Usnea*), numerous mosses, and a few ferns (e.g. *Polypodium* spp., *Vittaria lineata*), the following flowering plants are epiphytic in South Africa:

Orchidaceae: *Ansellia gigantea, Polystachya* (10 species), *Angraecum* (11 species), *Listrostachys arcuata*, and *Mystacidium* (9 species). Some of these are rather widespread, others very local in their distribution.

Amaryllidaceae: *Cyrtanthus epiphyticus.*

Piperaceae: *Peperomia reflexa, P. retusa.*

Gesneraceae: *Streptocarpus*, several species. *S. rexii* is one of the most widespread. The large single cotyledonary leaf spreads flat over the tree trunks and reaches a size of two and a half feet in *S. wendlandii*. The species of Streptocarpus, however, are not strict epiphytes. They require a certain amount of soil and occur also on the ground. This applies, to a certain extent, also to *Peperomia* spp. and some of the Orchids.

Scrophulariaceae: *Dermatobotrys saundersii.*

Cactaceae: *Rhipsalis cassytha*, a fleshy cord-like plant is often found hanging from trees, but occurs also on rocks.

Ficus natalensis begins its life as an epiphyte. The total number, even including species that are only sometimes epiphytic, does not exceed 45, a small total as compared with the hundreds that are found in the tropics. Not only are the epiphytic species few in South Africa, but they are also not abundant individually.

3. Parasites.—Parasites on trees and shrubs include *Cassytha* (Lauraceae) three species and *Cuscuta* (Convolvulaceae) eight species, but they are of little importance in the forest, occurring mostly outside it in grass-veld or Macchia. These two genera are very much alike in vegetative appearance, though they belong to such widely separated families.

The family of the Loranthaceae are much more important.

The genus *Loranthus* has 22 South African species, many occurring on a variety of hosts. It is, on the whole, distinctly more tropical than *Viscum*, being most prominent in the coast-belt bush of the eastern side. *Viscum* has 20 species well distributed over the whole of South Africa, and many of them very common in the eastern dry valley scrub and on the stream-bank trees and shrubs of the Karroo. Single species, again, often attack many different host plants.

Root parasites and hemiparasites are characteristic rather of grassland and Macchia, but may be dealt with briefly in this place. They include a large section of the Scrophulariaceae (the genera *Harveya*, *Hyobanche*, *Cycnium*, *Rhamphicarpa*, *Striga*, and *Melasma*). In addition there are *Cytinus* (Rafflesiaceae), *Hydnora* (Hydnoraceae), *Sarcophyte*, *Mystropetalon* (Balanophoraceae), *Orobanche* (Orobanchaceae), *Thesium* (128 species), and *Thesidium* (Santalaceae).

4. Undergrowth.—In evergreen tropical-subtropical forest, except near the margin or in open spaces caused by the death of old trees, very little light reaches the ground. Under such large-leaved species as *Xymalos monospora* or other hygrophilous South African trees the shade is so dense that there is no undergrowth even of mosses. Where the tree canopy itself is not absolutely a close one, any intervening gaps are very commonly filled in by the foliage of the various woody lianes already described, and there are no flowering plants to be found on the floor of the forest, except the seedlings of the dominant trees and of lianes, which often endure very dense shade.

Near the margin, however, or in the gaps already mentioned, the undergrowth may be rather luxuriant. Everywhere, under such conditions, the species found are extraordinarily closely allied to or identical with those occurring in marshy situations and along stream-banks. In South Africa comparatively few can be named that are confined to the forest. In more open scrub, tree-veld and xerophytic situations, the undergrowth consists largely of grass-veld plants, which are more or less mesophytic. The dominant trees and shrubs provide a certain amount of shade and shelter and a more humid atmosphere. Undergrowth generally, therefore, is more mesophytic or more hygrophilous than the dominant trees or shrubs with which it is associated.

We have seen that the herbaceous type probably first appeared in marshy places or near the moist forest margins. Adaptation to denser shade conditions has involved a modifying

of the normal physiological processes, with light as the limiting factor. Decreased assimilation is often at least correlated with slow respiration, but growth up to a certain stage may be rapid. Leaves are usually large, thin and membranous, though there are a few exceptions to this rule. Some of the shade-loving forest herbs may be very ancient, some belong to rather primitive families (*e.g.* Piperaceae and Araceae), but the vast majority are highly evolved, at least floristically (*e.g.* Acanthaceae, Labiatae, etc.). Wind-pollinated species are very rare, as is to be expected from the nature of the habitat. The flowers are mostly pollinated by shade-loving moths and butterflies. Even some of the trees and shrubs take advantage of these by producing flowers on the older parts of the branches underneath the canopy. This so-called cauliflory is seen in *Halleria* spp., *Rawsonia lucida*, and other trees in South Africa, and is much more common in the tropics.

Among wind-pollinated types there are a few grasses which also occur in vleis—*Panicum* spp., *Pennisetum* spp., and *Setaria* spp. (*S. sulcata* is rather common)—though none of them penetrate into very dense shade. Climbing forest grasses have already been dealt with. In the same class are a few straggling vlei sedges; *Cyperus albostriatus* is often very common in semi-open glades.

On the whole, the Monocotyledons are rather well represented, especially marsh species. Various species of *Zantedeschia* (Richardia), the Arum Lilies, can endure quite dense shade. In the Commelinaceae there are species of *Commelina* and *Aneilema*. Several of the Liliaceae occur, e.g. *Agapanthus umbellatus*, *Scilla* spp., etc. *Dracaena hookeriana* is an undershrub in the coast forests of Natal. Among the Amaryllidaceae *Crinum* spp., *Haemanthus* spp., and particularly *Clivia miniata*, the Bush Lily, have been very successful in solving the difficulties of a reduced light supply. Among the Orchidaceae there are found species of *Holothrix*, *Peristylus*, *Stenoglottis*, *Habenaria*, *Bonatea*, *Disperis*, *Disa*, *Brownleea*, and others.

Among the Dicotyledons the two most characteristic families are the Labiatae and Acanthaceae. In the former the large genus *Plectranthus* has 42 species recorded for South Africa, and the majority of them can endure shade. One of them is here illustrated (see Fig. 21), *Plectranthus peglerae*, with rather large leaves which grow up to eight inches long by four inches broad. It gives a good idea of the type of undergrowth in the more open glades of the Natal forests. Other Labiate genera

represented are *Orthosiphon*, *Iboza*, *Mentha*, *Salvia*, and *Stachys*. Among the Acanthaceae the genus *Justicia* is most prominent, but the whole family is predominantly of a forest margin herbaceous type, only a few of the genera being confined to the grass-veld and a few shrubby. Not very many, however, penetrate into dense shade. In open glades in the coast-belt forests of Natal they are very abundant. In addition to numerous species of *Justicia* there are species of *Isoglossa*, *Hypoestes*, *Dicliptera*, *Barleria*, *Blepharis*, *Thunbergia*, and others. Other genera and species are scattered through various

FIG. 21.—*Plectranthus peglerae* T. COOKE.
⅓ nat. size. Shade-loving plant of the forest undergrowth.

families, and only some of the most characteristic will be mentioned. There are at least seven species of *Begonia* fairly common. Among the Euphorbiaceae *Adenocline* (three species) and *Leidesia* (three species) are particularly characteristic, and there are also one or two species of *Euphorbia* and *Cluytia* genera much better represented in more open situations.

Impatiens capensis is very common in very moist spots. *Sanicula europaea* is another interesting and fairly common species. *Piper capense* is abundant in many forests, usually near streams in not very dense shade. *Streptocarpus* spp. are very characteristic, including about 20 species, most of which also occur as already mentioned, epiphytic on tree-trunks. Genera of the Malvaceae (*Hibiscus*, *Sida*, *Abutilon*, *Pavonia*), of

the Urticaceae (*Fleurya*, *Urera*), and of the Tiliaceae (*Sparmannia*) are confined to the more open spaces, where also occur a variety of stragglers from the grass-veld. Many vlei (marsh) species, which will be named later, are frequent, but the close connection of the undergrowth with this type has already been sufficiently insisted on.

Our knowledge of evolutionary history is still far too uncertain to enable a strictly logical arrangement of various subordinate types of plant growth form. Though the undergrowth of the forest may have originated much in the same way as the species inhabiting marshy situations (Helophytes), yet the two classes differ in their light requirements and, as a consequence, in their physiological processes and to a certain extent in their external appearance, though they are both herbaceous. To place all the herbaceous types together appears at first sight a more obvious and better arrangement. More, however, is lost than gained by it. The great key to evolutionary history, especially in an old continent like Africa, is the study of plant migrations, and each of the main types of plant community is best considered as a whole. Schimper's main subdivisions of vegetation were by far the most fundamental—woodland, grassland, and open or desert 'formations.' Many advances have been made in more recent years in the study of plant ecology. Successional studies have brought a much clearer understanding of the dynamic relationship between these main types of formation. If the climate permits, open types are succeeded by grassland types and these in turn by woodland types, but all differ fundamentally in their growth forms, a fact which renders plant succession possible. The types of growth form composing woodland have been considered first, but our study of these is not yet complete. Due value, however, has to be given to the historical factor. The trees and shrubs of the south-western and mountain regions of South Africa, since they have apparently had a distinct geographical origin, are to be considered separately later, after the grasslands and drier regions have been dealt with, so as to complete the history of the tropical-subtropical flora of South Africa. Various incidental comparisons, however, of the two floral elements are made throughout.

CHAPTER VII

GRASSES AND SEDGES

As already pointed out, one of the greatest problems in the evolutionary history of flowering plants is the origin of the grasses and the establishment of grasslands. Unfortunately, it is by no means an easy problem to solve. Though the grasses (*Phragmites*) are recorded for the Cretaceous, systematists are not agreed that they are to be considered primitive. Their embryos are very different from those of other Monocotyledons, and Agardh (1829) regarded them as the only true Monocotyledons. The rest of the group he called Syncotyledons, which, together with the grasses, made up what he called Kryptocotyledons, *i.e.* the group now generally recognised as Monocotyledons (see Bancroft, 1914).

Most modern systems of classification agree in uniting the grasses and sedges in the cohort or order ' Glumiflorae ' without attempting to find connecting links between the two families. Rendle (1904) appears to be inclined to the view that the Glumiflorae represents a primitive group and not a reduced type of Monocotyledon, though the grasses, he remarks, do show ' some degree of specialisation.' This, judging from the order of arrangement in his system, seems to meet the views of Engler. Of course, with the questions of origins remaining so obscure, there is a tendency in all systematic arrangements to adhere to accepted plans rather than attempt speculative systems of phylogenetic arrangement.

At the same time, there seems to be a growing consensus of opinion that the Glumiflorae are not primitive. The solitary ovule combined with either two or three styles suggests reduction and therefore derivation.

Wettstein (1898) derives all the Monocotyledons from the Dicotyledons (Polycarpicae) through the Helobieae, and the Glumiflorae from the Helobieae through the Liliiflorae. Lotsy (1911) also derives the Glumiflorae from the Liliiflorae, the two

families (Gramineae and Cyperaceae) independently from the Juncaceae.

All systematists, of course, base their conclusions on floral structure, but from the ecological standpoint the conclusions are of assistance, since the two families Gramineae and Cyperaceae are to be considered closely allied. There can be little doubt that of the two the Gramineae are the more specialised and recent.

Now, the Cyperaceae are almost entirely marsh types, as are a fairly large number of the Gramineae. This would seem to indicate that the whole of the Glumiflorae had a marsh origin. Before allowing ourselves, however, to accept this conclusion, we must investigate another possibility. We have already seen that marsh types and forest margin types are closely allied.

Arboreal growth forms are very rare in the whole group of the Monocotyledons, but they do occur, and Lindinger (1910) is of the opinion that such types as *Dracaena*, *Yucca*, and *Aloe* have retained ancestral characters in the purest form. This is in interesting agreement with the views of Sinnott and Bailey and others regarding the primitive nature of tree forms and the derivative nature of herbs. In the Glumiflorae the more primitive Cyperaceae are nearly all herbaceous, but *Schoenodendron* from West Africa (the Cameroons) is a small tree. Even in the Juncaceae, from which Lotsy derives the Glumiflorae, we have the woody-stemmed South African genus *Prionium*. Among the grasses the tree forms are the Bamboos, tropical and subtropical, usually forest margin and stream-bank types. Some of them are very tall; others, like the South African 'Berg Bamboo' (*Arundinaria tesselata*), are smaller and more like ordinary grasses.

The flower of the Bamboo among all the grasses comes nearest to the ordinary liliaceous type. Some of the Bamboos have a trimerous perianth, two trimerous staminal whorls, and an ovary bearing three stigmas. In most of the other grasses the only suggestion of a trimerous arrangement is the androecium of three stamens.

Whether we attempt to derive the Glumiflorae from woody tree-like ancestors or from herbaceous ancestors it seems fairly certain that the very early forms were hygrophilous and either forest margin or marshy types, and, as in the case of trees and shrubs, xerophytism was generally derivative. Dry grassland areas were not formed all at once and possibly not all in exactly the same way. In addition to the few modern tree forms in

the Juncaceae, Cyperaceae, and Gramineae, which are all mostly forest margin or marsh types, there is considerable diversity of other growth forms even in the same primitive types of habitat. There is the elongated many-noded stem often rooting at the nodes, the underground rhizome, and tufted forms, and all three types may have co-operated in the establishment of grasslands responding to the demands of increasing aridity.

The Cyperaceae.—Schönland (1922) lays emphasis on the fact that, as far as the South African Cyperaceae are concerned, 'the general liliaceous floral diagram is fully realised in *Macrochaetium* and frequently in *Tetraria* (sect. *Eu-Tetraria*), both confined to South Africa. These may be close to the original stock of the Cyperaceae.'

These forms are more or less confined to the south-western region, and if Schönland's suggestion is correct, the Cyperaceae supply another argument in favour of considering the mountain and south-western floral element in South Africa a very old one.

'*Schoenoxiphium*,' Schönland remarks, 'as circumscribed by Kükenthal is looked upon by that eminent authority as the starting point of the group of genera of which *Carex* is the most important member.' *Schoenoxiphium* thus defined contains eight species almost all endemic in South Africa, only *Sch. sparteum* var. *schimperianum* being also found in East Africa and Abyssinia and var. *lehmannii* also in East Africa.

In Natal it is frequently a forest margin genus. Schönland says that it grows often amongst grass. It is interesting to note that *Carex* has a cosmopolitan distribution, while the supposed ancestral type *Schoenoxiphium* has a relatively narrow distribution.

Schönland touches on certain other interesting general questions. Among the Cyperaceae of South Africa relations with the flora of Australia are found in *Schoenus*, which is mainly Australian, *Scirpus*, *Lipocarpha*, *Costularia*, and *Cyperus tenellus*. In South Africa these are mostly south-western and mountain types (*cf.* also C. B. Clarke, 1902). The monotypic *Macrochaetium dregei*, which inhabits the south-western coast district of the Cape, 'at first sight might be mistaken for one of the Restiaceae with the brown sheaths of its bracts in the floral region.' The members of the genus *Tetraria* also have 'all more or less a restiaceous habit which is especially striking in some species where the leaf-blade may not be developed (e.g. *T. punctoria* Nees). It is closely allied to *Epischoenus*,

Costularia, and *Macrochaetium*, but also to some exclusively or preponderatingly Australian genera with similar habit such as *Cyathochaeta* Nees, *Tetrariopsis* Clarke, *Schoenus* L., and *Caustis* R.Br. Taking these genera together, their distribution offers a close parallel to that of Restiaceae.'

The South African genera which are closely associated with tropical Africa are on the whole distinct from the south-western and include *Kyllinga*, *Pycreus*, *Juncellus*, *Cyperus*, *Courtoisia*, *Mariscus*, *Fimbristylis*, *Bulbostylis*, *Fuirena*, *Lipocarpha*, *Ascolepis*, *Scleria*, and *Eriospora*. The last four are only eastern and north-eastern in South Africa, though among the others there are many outliers in the south-west and among almost all of them many endemic species. *Cyperus* is the largest and commonest genus, followed closely by the nearly allied genus *Mariscus*. *Mariscus congestus* is the most widespread of all the species, occurring all over South Africa and in St. Helena, the Mediterranean region, and Australia. Other genera occurring in South Africa are cosmopolitan—*Eleocharis*, *Scirpus*, *Rhynchospora*, *Cladium*, and *Carex*.

Schönland divides the South African Cyperaceae into four groups of growth forms, but states that his arrangement is without systematic value.

(1) Forms with elongated, branched, many-noded stem (e.g. *Ficinia* sect. *Acrolepis*, *F. longifolia*, *F. capillifolia*, *Scirpus* subgenus *Fluitantes*). These may root at the nodes and may multiply by the older part of the stem dying off and setting the branches free.

(2) Small tufted forms producing branches at the base, which develop like the main stem without forming a distinct rootstock or elongated rhizome (e.g. *Cyperus tenellus*, *Scirpus sororius* and its allies).

(3) Larger tufted forms in which is found a distinct rootstock (caudex) from which numerous aerial stems arise. These are very common. In *Ficinia bulbosa* the rootstock is tuberous.

(4) Forms with a distinct elongated rhizome. These are also very common.

Special means of vegetative propagation are by (*a*) Stolons—frequently found in species with rootstock, though not always developed even when they normally occur. (*b*) Bulbs—in *Scirpus bulbiferus* and *Cyperus usitatus*. (*c*) Tubers—in *Cyperus esculentus* and *C. rotundus*. Since the habitat is so uniform it is very difficult even to guess at the possible evolutionary history of the different types of growth form. The

forest margin and vlei types often grow very tall and in the latter case gregariously, being completely dominant in all the wettest types of marsh. The smaller forms are scattered among the larger, and in South Africa such species as invade the grass-veld are also scattered, never dominant. They are subordinate to the grasses and presumably all derivative.

The Gramineae.—The general ecology and distribution of the grasses and the plant succession in South African grasslands have been dealt with in a former work (1918). The great subtropical grasslands of the whole eastern and northern portions of South Africa are dominated chiefly by members of the tribes Andropogoneae and Paniceae. The Rooigras, or Red grass, *Themeda triandra* (or *Anthistiria imberbis*), is dominant in the climax stages of the succession over immense areas. Associated with it are various species of *Andropogon*. The taller *Cymbopogon* species, Tambookie grasses, are more often transitional to forest or dominant in forest climatic areas, where the forest has been destroyed. They are also frequent in marshy situations. Species of Panicum are often ruderal or marsh or forest margin types. Species of *Pennisetum* and *Setaria* are usually hygrophilous; indeed, only a few of the Paniceae occur in drier types of grassland (e.g. *Panicum natalense*, *Axonopus semialatus*).

In the earlier stages of the (xerosere) plant succession species of *Aristida* (Stipeae), *Sporobolus*, and *Eragrostis* are dominant, but several of them mix with climax stages as well. With increasing aridity the plant succession does not proceed so far, and species of *Aristida* and *Eragrostis* are dominant in the climax stages over large areas of the interior. Members of the Pappophoreae (*Enneapogon* and *Schmidtia*) are also prominent in places. One of the effects of continuous grass-burning is continually to keep back the plant succession, and over large stretches early pioneer grasses like *Aristida* spp. remain dominant, though climatically the succession could progress further. When grass-burning is prevented the Aristidas give way to *Themeda* and the Andropogons.

The tribe Chlorideae include ruderal species (*Eleusine*, *Chloris*), sea-shore species (*Spartina*, *Dactyloctenium*), creeping pioneers on bare soils (*Cynodon*), and mountain species (*Microchloa*, *Harpechloa*). The Oryzeae, which are interesting because they usually have six stamens, have one shade-loving forest type, *Potamophila*, and one vlei grass, *Leersia*. Both habitats are primitive. The Arundineae, *Arundo* and *Phragmites*, are semi-

aquatic or marsh forms, and *Phragmites*, as already noted, is recorded from the Cretaceous. *Olyra latifolia* (Phareae) is another forest type from the Ngoya forest in Zululand. It has leaves 4 to 7 inches long by 1 to $2\frac{3}{4}$ inches broad with short hairy petioles, and the blades are transversely veined.

The Berg Bamboo (*Arundinaria*) occurs along the eastern mountain ranges in rather moist situations. The various types which show traces of the more primitive floral characters are distinctly hygrophilous. Little can be said regarding the phylogeny of the grasses, but if reduction in the number of florets in the spikelet has been a progressive tendency then the Andropogoneae and Paniceae are rather highly developed. *Aristida* is even more so. On the other hand, the tribes Aveneae and Festuceae, which are mostly temperate in distribution, having many florets in the spikelet, are possibly more primitive. At any rate, it is to the tribes Aveneae and Festuceae that the majority of the mountain and south-western grasses in South Africa belong. The tribe Phalarideae, which often has six stamens, is also chiefly south-western (*Phalaris* and *Ehrharta*). We have seen that some of the most primitive floral types of the sedges are south-western. The same may be true of the grasses. Since the grasses, as a whole, are to be considered a derivative group, it is more than likely that the temperate grasses are as old as, if not older than, the subtropical. The phylogeny of other families, as was indicated in Chapter III, would support this view, especially that of the allied family the Cyperaceae. Further reference to the south-western grasses will be made when the whole south-western flora is dealt with, but their growth-form characters will be considered with those of the subtropical regions, since in the south-western region they play a subordinate rôle to the Fynbosch shrubs.

There is considerable diversity of detail in the growth forms of grasses, though, with the exception of the Bamboos, there is such general uniformity. The features common to nearly all are the main characters of leaf sheaths, ligules and blades, the arrangements of the leaves in two ranks, the branching of the stem at the base producing tufts erect or of ascending, prostrate or creeping, simple or ramified branches. The internodes are usually (but not always in the Andropogoneae and one or two others) hollow. The basal internodes are usually much shortened, the upper internodes lengthened. The innovation shoots, which grow into culms as a rule in the

second year after they are formed, are either intravaginal or extravaginal and produced into runners or stolons.

The variations of growth form are largely to be correlated with variations in habitat, and the arrangement here followed indicates in a very general way their possible evolutionary history.

1. The Bamboos. These woody types are clearly in a class by themselves. The only South African example, *Arundinaria tesselata*, the Berg Bamboo, is interesting, because its stamens are reduced to three, while all the tropical genera except *Microcalamus* have six. *Arundinaria* in South Africa is a small form, usually found along mountain streams. Some of the other grasses, e.g. *Erianthus*, grow as tall or taller. In the tropical regions, however, the Bambusoideae are much more highly differentiated, and this, combined with their wide distribution, is an argument in addition to their primitive floral character for considering them ancient forms. The tribe Melocanneae have the fruit a nut or berry, with a thick pericarp free from the seed. It is represented by *Schizostachyum*, a Madagascar monotypic shrub with the fruit a small wrinkled nut. *Melocanna*, with a large apple-like berry, is naturalised in Mauritius. It reaches tree size. *Cephalostachyum* is another monotypic Madagascar genus with two to three large lodicules. *Nastus* has three species (Madagascar and the Mascarenes). In West Africa and the Cameroons there are a number of more or less herbaceous genera of Bamboos, *Microcalamus*, *Atractocarpa*, *Puelia*, *Microbambus*, and *Guaduella*. *Oxytenanthera* (five species of tall shrubs) is Central African, and *Oreobambus* and *Arundinaria* are East African. Species of *Bambusa* are cultivated and often naturalised.

2. Tall-growing hygrophilous (marsh and forest margin) types. Examples: species of *Arundo*, *Phragmites* (the reed grasses), *Erianthus* (umTala), *Cymbopogon* (Tambookie grasses), *Pennisetum*, *Setaria*. The growth forms of this class are undoubtedly ancient and in some respects suggest those of the Bamboos. *Phragmites* often takes complete possession of long stretches of river-banks. The Tambookie grasses are often completely dominant in a wide belt around the forest margins, growing up to 10 feet or even higher. The Elephant grass, *Pennisetum purpureum*, is abundant in the tropics, growing up to 15 or 20 feet high (see Monteiro's account quoted in Chapter III). *Setaria sulcata* is rather common around the

forest margins in Natal or in open spaces within the forest. *Phragmites* is widely dispersed over the world, the others are tropical-subtropical (*Arundo* is probably introduced in South Africa).

3. Hygrophilous tufted grasses. These are often dominant in South African vleis, e.g. *Agrostis lachnantha*, *Arundinella eckloni*, *Eragrostis nebulosa*, *Pennisetum* spp., *Setaria* spp., *Diplachne fusca*. They have often short oblique rhizomes, and compare in some respects with the growth forms of the sedges with which they are associated. They occur also along the forest margins. They suggest a possible origin for the bunch grasses.

4. Hygrophilous straggling or creeping grasses, often rooting at the lower nodes, with the upper parts of the stem ascending. These are found in vleis, but are more common along the forest margins. Examples: *Leersia hexandra*, which is sometimes dominant in vleis; numerous species of Panicum (*P. filiculme*, *P. hymeniochilum*, *P. aequinerve*, *P. perlaxum*, *P. chusqueoides*, *P. obumbratum*, *P. laticomum*, and *P. zizanioides*) which are common around the subtropical coast-belt forest of the eastern side; *Ischaemum fasciculatum* var. *arcuatum*, *Rottboellia compressa* var. *fasciculata*. This class of growth form connects very closely with the next two or three groups, climbing grasses, surface-rooting pioneer types in the xerosere and psammophilous grasses, and also suggests an origin for the sod-forming grasses. Though the marsh type of habitat is an ancient one, of course many hygrophilous grasses may be of recent phylogenetic origin, since there is no reason why new species should not adapt themselves to moist conditions.

5. Climbing grasses and shade-loving scrambling forest species. Examples: *Panicum* spp., *Olyra latifolia*, *Pollinia nuda*, *Potamophila prehensilis*, *Brachypodium flexum* var. *simplex*, *Stipa dregeana*. A derivative class, though, like other climbing plants, possibly very ancient.

6. Creeping surface-rooting grasses and psammophilous species. There are certain species which show connections between marshy habitats and sandy. *Eragrostis glabrata*, *E. elatior*, and *E. sarmentosa* grow in both. *Eragrostis cyperoides* is a litoral sand-dune species. These are all south-western. *Eragrostis spinosa* is a creeping spiny type with long rhizomes or stolons, very common in the dry plains of the interior and western side. It is the Vogelstruis or Ostrich grass. *Spartina*

stricta is a rather rare creeping stoloniferous seashore species found at Port Elizabeth and Port Alfred. It also occurs along the shores of Europe. *Sporobolus pungens* is another creeping sand-dune and seashore grass widely distributed along the shores of most warm countries. Its internodes are alternately very short and long, so that its leaves appear opposite. *Stenotaphrum glabrum* grows in moist soil or on sandy flats near the seashore from the Cape to Natal. It is a creeping type rooting from the nodes and is often used for making lawns. *Dactyloctenium aegyptiacum* is similar in its behaviour and ecology. It extends along the eastern side as far as Port Alfred, but it is widespread through the tropical-subtropical regions of the world. *Cynodon dactylon* is one of the most important pioneers on bare spaces, along roadsides, over ant-heaps, etc., all over the eastern side. *C. incompletus* is similar but more xerophytic and is distributed over the drier parts of the interior and west. *Cynodon* spp. have creeping stems, rooting at the nodes and emitting from them fascicles of barren shoots and flowering culms. They are largely used as lawn grasses in South Africa. *Schmidtia bulbosa* (Zand Kweek gras) is one of the most important species in the sand-veld of the Kalahari and western Free State and Transvaal. It is a tufted form with numerous villous conical innovation buds. Hence the base is more or less bulbous.

While the xerophytic creeping type is obviously closely similar to the same type among the hygrophilous grasses, the fact that roots can be formed at every node makes it peculiarly suited to act as a colonising type over bare spaces. The Cynodons and others that act in this way are intense light-demanders. They are soon killed by taller-growing tufted grasses, a fact that is familiar to everyone who has used them for making lawns. They are found, naturally, only in the very earliest stages of the plant succession. Creeping grasses are also well suited to growing through sand, which they help to bind. Roots again are formed usually from every node. The introduced Marram grass, *Ammophila arundinacea,* has been planted in many places as a sand-binder along the coast sand dunes.

7. Stoloniferous sod-forming grasses. Though in addition to the last class many of the South African bunch grasses are also stoloniferous, hardly any of them can be described as true sod-formers. Sod grasses are more characteristic of the cool temperate regions of the world. South African species of

Poa, *Festuca*, *Agrostis*, etc., occur very sparsely scattered through the other dominant grasses or shrubs, and it is the common experience that introduced sod-forming grasses from the northern hemisphere do not thrive in South Africa, though *Agrostis stolonifera* and *Poa pratensis* are sometimes used for making lawns. The stoloniferous habit was probably evolved very early in the evolutionary history of the grasses, but in the tropical-subtropical species the stolons do not branch very freely through the soil.

8. Mesophytic bunch grasses. Examples: Species of *Themeda*, *Andropogon*, *Urelytrum*, *Panicum* (*P. natalense*, *P. eckloni*, etc.), *Tricholaena*, *Trichopteryx*, *Agrostis*, *Sporobolus*, *Eragrostis*, *Digitaria*, etc. These are the dominant grasses of eastern and northern grass-veld areas at the climax stages of succession. They grow in tufts close together, completely covering the surface of the soil, and when flowering are usually three or four feet in height. They are mesophytic in contrast to the deep-rooted pioneer wire grasses, etc. Their leaves are not very fibrous and in cross-section do not show the prominent sclerenchymatous ridges with grooves in between, seen in more xerophytic types. There are no motor cells, and their leaves with few exceptions remain flat and do not roll up from the margins in dry weather. There is, however, often a considerable development of large water-storage cells along the upper side of the leaf and particularly above the midrib. These grasses are palatable to stock and more nourishing than the wire grasses, and in my 'Grasses and Grasslands' book it was suggested that the feeding value of South African grasses could be gauged from the degree of softness of the leaves, *i.e.* the relatively poor development of fibre or sclerenchyma. Various figures of cross-sections of leaves were given to illustrate the working of the principle. All that is required is to section the leaf to get a rough idea of the value of the grass. The conclusions reached have now been confirmed by very careful chemical analyses of the herbage of Natal grasses throughout the year, carried out by Mr. A. J. Taylor (1922). The various series in which he arranges them show that their nutritive value varies more or less inversely with their fibre content, and their fibre content as tested by chemical analyses agrees very well with the estimates obtained by microscopical examination. A glance through the figures reproduced in my work referred to show that *Themeda* (*Anthistiria*), *Andropogon*, *Chloris*, *Digitaria*, *Setaria*, *Harpechloa*,

Tricholaena, and *Tristachya* are all remarkably free from sclerenchyma. *Urelytrum* has slightly more fibre. These are all subtropical types. *Eragrostis*, a pioneer type, has much more sclerenchyma with motor cells as well. The large amount of water-storage tissue in *Harpechloa capensis* is particularly noticeable. The figures given for the typically pioneer and xerophytic genus *Aristida* and for the mountain and South-western genera (*Achneria, Danthonia, Pentaschistis, Ehrharta, Lasiochloa*) differ in their excessive development of fibre, deep grooves, and motor cells. There is room for much further work on the leaf anatomy of the grasses from the evolutionary standpoint as well as from the purely economic.

FIG. 22.—*Eragrostis chalcantha* TRIN.

½ nat. size. Common pioneer grass in eastern grass-veld.

9. Tussock-forming grasses. Examples : *Microchloa* spp., *Harpechloa capensis, Panicum eckloni, Sporobolus festivus* var. *stuppeus, Eragrostis* spp., and under appropriate conditions many of the last class. It is doubtful whether these ought to be separated from the Bunch grasses. They differ only in forming much harder tufts with the soil tending to become heaped up between the culms, while bare spaces are left between the tussocks. Tussock-veld is characteristic of the foot-hills of the Drakensberg. Its character is best seen in spring before the more subtropical bunch grasses take possession.

10. Xerophytic bunch grasses. Examples : Species of *Aristida, Eragrostis, Sporobolus, Elionurus, Enneapogon, Fingerhuthia, Oropetium, Tetrachne, Danthonia, Pentaschistis, Achneria, Lasiochloa*, etc. *Aristida* is by far the most prominent genus among these. On the

great sandy plains from the South-Western Protectorate through Calvinia, Gordonia, and Prieska the Toa grass (*Aristida brevifolia*), a very xerophytic suffrutescent species, covers great areas, while in the transitional belt between Karroo and eastern grass-veld the 'Steek gras,' *Aristida congesta*, is the chief species. It is dominant over large stretches of the western Free State. The whole of the *Stipagrostis* section of the genus *Aristida* consists of semi-desert species. The other sections of the genus are more prominent in the transitional areas to grass-veld, or, like *A. junciformis*, *A. angustata*, etc., are dominant in the early stages of the plant succession over the eastern side. They often remain dominant as a result of grass-burning. The leaves of all the species of *Aristida* are full of fibre, some of the desert species extremely so. *Cf.* also the spiny *Eragrostis spinosa* already described.

The increase of fibre content in grass leaves corresponds exactly to the similar increased lignification in the assimilating organs, thorn development, etc., in the trees and shrubs, which we found to be one of the main evolutionary responses to increased aridity. Among nearly all the xerophytic bunch grasses the leaves tend to be of the setaceous type, contrasting with the flat, smooth, tapering linear leaves of the mesophytic types.

Though some of the south-western grasses are creeping, straggling, or psammophilous types, the majority are xerophytic bunch grasses. In many of them xerophytism reaches an extreme development, *e.g.* in *Ehrharta aphylla*, where the leaves are absent altogether and the culms are woody at the base. A half-suffrutescent habit is common in many of them. Floristically and otherwise they may be rather ancient.

11. Annual grasses. The majority of these are ruderal species characteristic of waste spaces, roadsides, etc., or of cultivated land. Many of the so-called 'land grasses' which grow up after the mealie crops are reaped are among the most nutritious grasses in South Africa. On the eastern side *Eleusine indica*, *Panicum* spp., *Digitaria* spp., *Setaria* spp., *Chloris* spp., and *Tricholaena rosea* are common. They are all tropical-subtropical species and often behave as sub-perennials.

A few of the subtropical types penetrate into the south-western region, for annuals tend to become very widespread, e.g. *Digitaria sanguinalis*, *Panicum crus-galli*, *Setaria verticillata*, *Eragrostis aspera*, *Eleusine indica*. Ruderal grasses ear also fairly common in the drier regions of the Karroo and

west. *Stipa tortilis* is a semi-desert annual very common in parts of Namaqualand and the south-west.

At the Cape there is a greater variety of temperate genera and species, most of them probably introduced, e.g. *Bromus* spp., *Vulpia* spp., *Lolium* spp., *Briza* spp., *Avena* spp., *Hordeum murinum, Holcus setiger, Brachypodium distachyum, Cynosurus echinatus, Lagurus ovatus, Trisetum pumilum, Phalaris minor, Koeleria phloeoides.*

As in the case of other annual plants, the annual grasses are probably the most recent, being characteristic of situations disturbed by man or of desert regions.

CHAPTER VIII

SUBORDINATE TYPES

Marsh plants (Helophytes)—Water plants (Hydrophytes)—Seashore strand plants—Associated plants of the grass-veld.

The two main classes of tropical-subtropical growth forms have now been dealt with, the woodland types and the grassland dominant types. An origin for them all has been sought for in moist tropical forest or in hygrophilous marshy habitats or, in a few cases, on the seashore. Just as a number of other types of growth form, besides the trees and shrubs, are associated with forest and scrub, including climbing plants, epiphytes, and herbaceous undergrowth, so in grassland areas there are many other types besides the grasses and their allies, the sedges. Many of those connect with the trees and shrubs in a more obvious way than the grasses and sedges. There are examples of herbaceous or suffruticose grassland species which belong to genera which are predominantly arboreal.

In various systems of classifying growth forms, marsh plants (Helophytes) and aquatic plants (Hydrophytes) are recognised as distinct classes. This is really purely a habitat classification, and there is no good reason why grassland plants should not be recognised in the same way. It is true that grasslands are not so uniform, and such a class would have to be subdivided. By dealing with the grasses and sedges first of all separately, the evolutionary aspect of our subject is given greater prominence, which is one of our present objects.

A very large number of the subordinate associated grassland plants belong to the class of geophytes, others are hemicryptophytes or chamaephytes, and a few that are really transitional to scrub are to be classed as nanophanerophytes. The dwarf shrubs and succulents become increasingly important in the drier regions until they become completely dominant in the Karroo, but these will be dealt with in the next chapter.

The various subordinate types at present under consideration are in some respects rather heterogeneous, and lengthy enumerations of them will not be attempted. At the same time, a sufficient number of them will be referred to to emphasise their diversity, and some of the more interesting will be considered in greater detail.

Marsh Plants (Helophytes).—The dominant marsh plants are the various Cyperaceae and Gramineae already described. In the south-western region the Restionaceae are also often marsh types. Altogether in these three families there are at least 500 helophytic South African species. Other Monocotyledons are also very characteristic of the same habitat, particularly numerous Orchids and such genera as *Kniphofia* (the Red-hot Poker) among the Liliaceae. Probably not less than 800 Monocotyledons occur in South African vleis, or about 25 per cent. of the total South African species belonging to the group. The helophytic Monocotyledons are much more numerous than the purely aquatic or hydrophytic, though in the case of semi-aquatics it is rather difficult to draw an exact line between these and marsh plants. Henslow (1893, 1911) has sought for an origin for Monocotyledons from Dicotyledons through 'self-adaptation to a moist or aquatic habit.' So far as a purely aquatic origin for Monocotyledons is concerned the evidence is entirely insufficient, for the numbers are relatively few and it is doubtful whether, except in rare cases, species which have once become aquatic have ever again given rise to types which, like the grasses, etc., are capable of colonising dry land surfaces. An origin for Monocotyledons in moist habitats, as distinct from aquatic, is quite probable, but it has little force as an argument that they have been derived from Dicotyledons, since all the Angiosperms, as a group, would appear to have originated under moist conditions.

Marsh plants belong to a great variety of widely separated families. Among the Dicotyledons they are more scattered and isolated than among the Monocotyledons, and it is only in the latter that there are large families predominantly helophytic. Some marsh plants are primitive in their floral characters. The Ranal order is fairly well represented, and the Sympetalae are not proportionally more abundant than the Archichlamydeae as they are in the undergrowth of the forest. Nearly all the Monocotyledonous orders are represented. This wide representation among different circles

of affinity shows the ancient character of the habitat, but not necessarily the ancient nature of all the plants inhabiting it.

In addition to the Cyperaceae and Gramineae already dealt with, and the Restionaceae, which will be referred to in connection with the south-western vegetation, the following list will give some idea of the more common examples of South African marsh plants.

Araceae: *Stylochiton* spp., *Zantedeschia* spp.

Commelinaceae: *Commelina* spp.

Typhaceae: *Typha capensis*, *T. australis*.

Scheuchzeriaceae: *Triglochin* spp.

Hydrocharitaceae: *Lagarosiphon muscoides*.

Juncaceae: *Juncus* (28 species), *Luzula africana*, *Prionium palmita*.

Xyridaceae: *Xyris* (8 species).

Eriocaulaceae: *Eriocaulon* (7 species).

Liliaceae: *Kniphofia* spp.

Amaryllidaceae: *Crinum* spp., *Anoiganthus breviflorus*.

Iridaceae: *Romulea* spp., *Tritonia* spp., *Gladiolus* spp.

Orchidaceae: Species of *Eulophia*, *Brachycorythis*, *Satyrium*, *Habenaria*, *Disa*, *Pterygodium*, *Disperis*, and others.

Ranunculaceae: *Ranunculus* spp.

Polygonaceae: *Polygonum* spp., *Rumex* spp.

Chenopodiaceae: *Chenolea diffusa*, *Salicornia* spp., saline (seashore) types.

Cruciferae: *Nasturtium* spp.

Droseraceae: *Drosera* spp.

Crassulaceae: *Crassula* spp. (especially sect. *Tillaea*).

Rosaceae: *Geum capense*, *Alchemilla* spp.

Leguminosae: Species of *Psoralea*, *Indigofera*, *Lessertia*, *Crotalaria*.

Geraniaceae: *Geranium* spp.

Oxalidaceae: *Oxalis* spp.

Euphorbiaceae: Species of *Phyllanthus*, *Cluytia*, *Acalypha*

Guttiferae: *Hypericum* spp.

Lythraceae: *Nesaea* spp.

Melastomaceae: *Dissotis* spp.

Oenotheraceae: *Epilobium* spp., *Ludwigia* spp.

Halorrhagaceae: *Gunnera perpensa*.

Umbelliferae: *Hydrocotyle* spp., *Sium thunbergii*.

Ericaceae: *Erica* spp. (rarely).

Gentianaceae: *Sebaea* spp., *Chironia* spp.

Borraginaceae: *Myosotis* spp.

Labiatae: *Mentha* spp., *Teucrium* spp., *Plectranthus* spp., *Orthosiphon* spp.

Scrophulariaceae: Species of *Sutera, Zalusianskya, Limosella, Phygelius, Sopubia, Ilysanthes, Diclis.*

Gesneraceae: *Streptocarpus* spp.

Lentibulariaceae: *Utricularia* spp.

Rubiaceae: Species of *Anthospermum, Galium, Oldenlandia.*

Valerianaceae: *Valeriana capensis.*

Campanulaceae: *Lobelia* spp., *Wahlenbergia* spp.

Compositae: Species of *Nidorella, Athanasia, Helichrysum, Senecio, Ursinia, Matricaria, Adenostemma.*

The Dicotyledons are very seldom dominant in South African vleis, and the total number of dicotyledonous helophytes is considerably less than the monocotyledonous, since the sedges, grasses, orchids, Restionaceae, etc., all help to swell the numbers of the latter. If the total South African flora be taken as about 13,600 species, probably not less than 1100, or between 8 and 9 per cent., are marsh plants. When the classification of plant growth forms was discussed it was stated that Raunkiaer gives only 1 per cent. for both helophytes and hydrophytes together. There must be some mistake in this estimate. South Africa can hardly be described as a peculiarly moist or marshy country. There are no sheets of fresh water of any size, and the rivers in general are steep-graded. There are, of course, countless small vleis of all kinds and they occur at varying altitudes from sea-level up to 11,000 feet and in every kind of climate. This may explain to a certain extent the considerable diversity in marsh vegetation, but it is extremely unlikely that South Africa has eight or nine times the normal number of marsh plants in the whole world's flora. This is leaving out of account the purely aquatic species, which would still further increase the total.

The species included in the present class are all herbaceous or suffruticose, since the hygrophilous trees and shrubs have already been considered. It is probable that moist, marshy habitats saw the origin of the most ancient herbaceous types among Angiosperms, but after the development of the grasses and the establishment of grasslands there was room for much greater differentiation among herbs. The geophytic type with underground storage multiplied exceedingly then, but its beginnings are seen in marshy situations. Creeping stems and underground rhizomes are particularly common among helophytes. The growth forms of the dominant sedges and

grasses have already been given. The other plants are subordinate to them. Though some of them doubtless are primitive, it must not be assumed that the majority are. The fact that they are sparsely scattered through so many different families would be against such a view. Many of them belong to large genera the bulk of whose species are not marsh plants. It is interesting to note that even in such a typical xerophytic genus as *Erica* a few of the species are hygrophilous. In the genus *Crassula* the section *Tillaea*, considered by Schönland to be the most primitive, is either mesophytic or hygrophilous.

One of the most interesting of the genera included in the above list is *Gunnera*, owing to its being polystelic and having very large leaves. Scott (1890) put forward a theory regarding this. Aquatic plants have their vascular system greatly reduced and usually centrally placed, and they generally have lost their cambium. If any aquatic returns to terrestrial life it has difficulty in renewing its cambium. Instead of doing so, it meets the increased demand for a vascular carrying system by multiplying the number of separate steles. This is what is supposed to have happened in the case of *Gunnera*. It has aquatic relatives at the present day, and it has probably descended from aquatic ancestors. Other polystelic genera are similar, and similarly have aquatic affinities. But if polystely is a necessary result of the descent of terrestrial plants from aquatic ancestors it must have been a very rare occurrence.

Mrs. Arber (1920) has elaborated a 'Law of Loss' in evolution similar, as she herself points out, to Dollo's 'Law of Irreversibility' as applied to animals. It is that as a general rule a structure or organ once lost in the course of phylogeny can never be regained. She applies it to many features in water plants, for details of which her book should be consulted, including the case of *Gunnera* and other polystelic types. The most important application of the principle is to the phyllode theory of the origin of monocotyledon leaves, first put forward by De Candolle as early as 1827. If this theory is true, then the ordinary type of leaf lamina was first of all discarded by Monocotyledons and afterwards replaced by a modification of the petiole.

The South African Araceae, like the majority of the subtropical members of the family, are swamp plants, usually with large sagittate or cordate leaves. In many places *Zantedeschia aethiopica* (*Richardia africana*) is completely dominant, forming one of the most showy of the vlei associes. Even more striking

are the numerous species of *Kniphofia*. Species of *Crinum* usually grow more or less sparsely scattered, like the various vlei Orchids. The vlei *Utricularias*, unlike the aquatic species, have no bladders. *Lobelia* spp. are rather common, small delicate herbs growing round the margins like many others mentioned in the above list, *Oxalis* spp., *Crassula* spp., *Geranium* spp., etc. Some of the *Dissotis* spp. have rather showy flowers and velvety leaves with intramarginal veins. Altogether many of the most beautiful flowers of the whole South African flora are included among the vlei types.

Halophytes might be separated as a distinct class, since the saline nature of their habitat renders them physiological xerophytes, but from the evolutionary standpoint adopted in this work it is hardly worth while. Very many of the species found around the margins of brackish lagoons at the river mouths also occur in freshwater vleis, e.g. *Triglochin* spp. Two halophytic genera are mentioned above *Chenolea* and *Salicornia*, both common on seashore mud-flats. The halophytic marshy habitats are equally or even more ancient than the freshwater, but the number of obligate halophytes in South Africa is small. The dominant mangroves have already been dealt with, and some of the strand halophytes will be referred to later.

The main growth-form characters of marsh plants may be summarised briefly.

1. Nearly all the species are perennial herbs.

2. The dominant species are nearly always Monocotyledons (grasses, sedges, Restionaceae, Typha, etc.).

3. Underground creeping rhizomes with adventitious roots fix the plants very firmly in the shifting soil and cause dense social growth, producing pure associes.

4. The aerial stems are usually unbranched and end in inflorescences.

5. Many of the Dicotyledonous species are small creeping forms, others are weak stragglers.

6. A few species are slightly woody and remain subordinate types, but when woody shrubs take possession the succession has passed to hygrophilous scrub, which in turn gives way to forest.

7. Some marsh species are xeromorphic, *i.e.* they have a xerophytic appearance, but it is uncertain how far they really should be classed as xerophytes (even as physiological xerophytes), for their rates of transpiration, in spite of their

appearance, may be high. Coverings of hairs on the leaves, for instance, are fairly common, and reduction of the transpiring surface is also frequent. These features may be useful in enabling the plants to survive during occasional drying-up of the soil water, a frequent occurrence in South African vleis. Among the Cyperaceae Schönland (1922) calls attention to the fact that South Africa is particularly rich in species which grow in localities that are subject to periodic intense drought.

8. The majority of marsh plants have a well-developed aeration system in response to lack of air in the substratum. With a few exceptions their leaves are mesophytic.

9. There is an absence of succulence except among the halophytic species, and in general an absence of spinosity and other more pronounced xerophytic characters of the vegetation of dry climatic areas. The provision made for underground storage is not pronounced, though food is stored in the underground rhizomes. Bulbous and tuberous plants are rare even in families where they are predominant elsewhere. *Kniphofia* (Liliaceae), for instance, is neither bulbous nor tuberous. *Crinum* spp. (Amaryllidaceae), however, have large bulbs, and various Orchids are tuberous. These are all more recent phylogenetically and occur around vlei margins or in relatively drier spots. In moist marshy habitats there is not the same necessity as in dry grassland areas for making provision for the long dry resting season. Climate, however, does have an effect even on marsh vegetation, and the beginnings of various responses to dry winters are seen especially among the more derivative marsh types that are not confined to the wettest parts. These may all be looked upon as transitional to dry grassland types.

Water Plants (Hydrophytes). — These are probably all derivative. Mrs. Arber (1920) in her book on 'Water Plants' gives a biological classification based on an earlier scheme of Schenck (1885), showing various degrees of adaptation to water life. She states also that 'there is good reason to assume that the Angiosperms were originally a terrestrial group, and hence that the aquatic Flowering Plants existing at the present day can trace back their pedigree to terrestrial ancestors.' At the same time, she points out that any classification of aquatics on biological lines is highly artificial and only has an indirect bearing on questions of phylogeny. This, of course, at the present state of our knowledge applies to all growth-form classification, though the subject has possibilities

that may be more fruitful from the evolutionary standpoint even than the study of floristics.

The plants which are not rooted in the soil but live unattached in the water, being farthest removed from the terrestrial mode of life, are considered the most highly specialised of water plants. The plants which are rooted in the soil include all gradations, from some essentially terrestrial plants that are able to live in water without marked adaptation, through amphibious forms with two or three different kinds of leaves, to those that are essentially aquatic. The latter may have leafy aerial shoots above the level of the water or may only have aerial inflorescences. They may be with or without the floating type of leaf, the upper surface of which is exposed to the air, or finally may be entirely submerged with hygrophilous pollination. This system probably shows the essential stages of adaptation to a purely aquatic life, if we assume that all aquatic forms are derivative from land forms. At the same time, among the Helobieae there are included many essentially very primitive forms whose terrestrial ancestors, if these were Angiospermous, have probably entirely disappeared.

In South Africa the whole group of aquatics are, on the whole, individually rather scarce, but representatives of most of the typically aquatic genera of temperate regions are found, and, in addition, there are interesting examples of tropical types, *e.g.* the Podostemads. The South African hydrophytes are distributed among the families as follows :

Monocotyledons

Potamogetonaceae: *Potamogeton* (11 species, 6 species with and 5 without floating leaves), fresh or brackish water. *Ruppia spiralis*, at the Cape, submerged brackish water plant. *Zannichellia palustris*, submerged fresh or brackish water along the coast, but also occasionally inland. *Zostera marina* var. *angustifolia* and *Zostera nana*, submerged marine aquatics.

Naiadaceae: *Naias interrupta*, submerged Transvaal aquatic. *Naias* is considered by Rendle (1899) to be a primitive type of Monocotyledon.

Hydrocharitaceae: *Lagarosiphon muscoides* var. *major* (semi-aquatic).

Aponogetonaceae: *Aponogeton* (9 species), submerged

plants with tuberous root-stocks, some species also terrestrial and inflorescence always aerial. This genus possibly forms a connecting link between the Helobieae and the Spathiflorae.

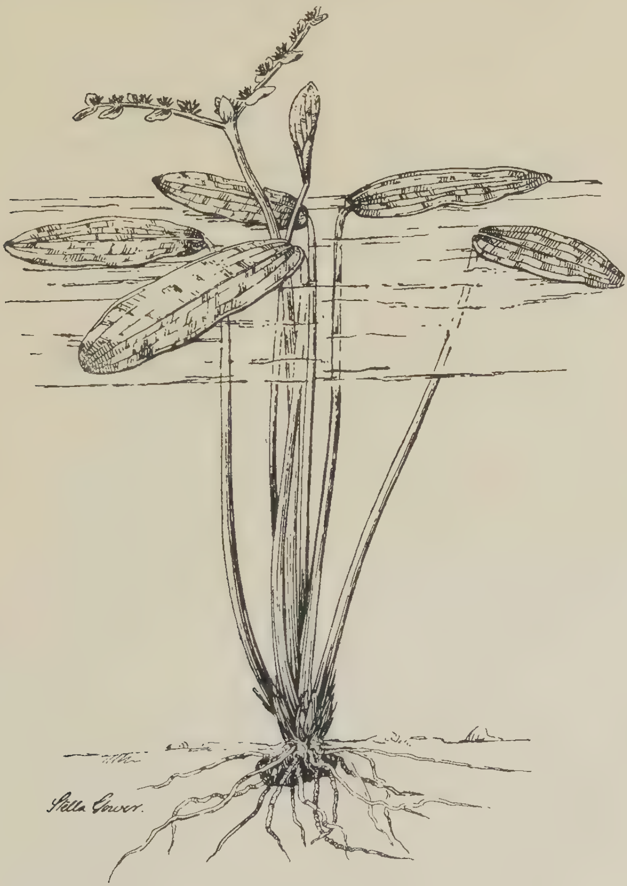

FIG. 23.—*Aponogeton distachyon* HOOK. f.
½ nat. size.

Araceae : *Pistia stratiotes*, a floating aquatic in Natal rivers; also tropical.

Lemnaceae : *Lemna minor* and *L. gibba*, minute floating forms with one or two floating roots on their under surfaces. *Wolffia michelii* and *W. denticulata* similar but rootless.

Cyperaceae : *Scirpus* sect. *fluitantes* and *S. lacustris*, but it

is not easy to draw the line between aquatic and marsh forms in this family. The same applies to the Typhaceae, Juncaceae, Xyridaceae, Eriocaulaceae, and Juncaginaceae. See above under Marsh Plants.

Pontederiaceae: *Heteranthera kotschyana*, an interesting tropical species from the Transvaal. Lower part of stem creeping or rooting in the mud. Leaves all linear and submerged or with long petioles and cordate, ovate, or reniform blades.

Dicotyledons

Ceratophyllaceae: *Ceratophyllum demersum.*

Nymphaeaceae: *Nymphaea* (2 species).

Podostemonaceae: *Sphaerothylax algiformis*, recently rediscovered in the upper Umzindusi, near Maritzburg, growing on dripping rocks.

Tristichaceae: *Tristicha hypnoides*, common, submerged.

Hydrostachyaceae: *Hydrostachys natalensis*, fairly common, submerged.

Crassulaceae: *Crassula natans.*

Callitrichaceae: *Callitriche bolusii* and *C. compressa.*

Oenotheraceae: *Jussieua repens* (*fluitans*) and *Trapa bispinosa.*

Halorrhagaceae: *Myriophyllum spicatum.*

Gentianaceae: *Limnanthemum thunbergianum.*

Scrophulariaceae: *Limosella aquatica.*

Lentibulariaceae: *Utricularia*, four or five species with bladders, the others being terrestrial. *Genlisea hispidula*, bladders tubular with two spirally twisted arms.

It is remarkable how few of the South African aquatics belong to the Sympetalae. There are only about half a dozen, unless one or two semi-aquatics are added. This is in sharp contrast to the undergrowth of the forest. The Dicotyledonous aquatics are only half as numerous as the Monocotyledonous. In these, as in other features, the South African aquatics agree with the group in the world as a whole. Their main growth-form characters and structural peculiarities are well known. They are usually perennials, either rootless (in floating forms) or fixed in soil by roots which, however, then do, as a rule, function as absorptive organs and only sometimes are reduced to mere fixing organs. The water-conducting system is reduced in amount and usually centrally placed. Secondary

growth in thickness rarely takes place, there being often no functional cambium.

The occurrence of chlorophyll often in the epidermis is to be correlated with the diminished light supply. Mechanical tissue (sclerenchyma) is rarely present to any extent, since water is a denser medium than air. What fibre is present is placed near the centre of the stem, so as best to resist tensile stresses.

The aeration system is well developed in water plants, the intercellular spaces being often very large.

Extreme modification is seen in the minute Algal-like forms such as *Lemna* and *Wolffia*, and also in the Podostemads and their allies (*Tristicha*), where the whole plant is often reduced to a thallus.

Seashore Strand Plants.—The various hygrophilous halophytes, trees, shrubs, and herbs, have been included with other hygrophilous types, though it was recognised that the presence of salt in the water introduced a disturbing factor leading to physiological xerophytism. Sand-dune shrubby species have also been included among the scrub vegetation. The important seashore grasses have been mentioned.

There remain a few halophytic, herbaceous or suffruticose species, many of which are very widespread along tropical seashores. Since practically the whole coast-line of South Africa is sandy, they are nearly all psammophilous halophytes with creeping stems, rooting at the nodes and helping to bind the sand. Only a few of the most important need be mentioned: *Hydrophylax carnosa* (Rubiaceae), *Scaevola thunbergii* (Goodeniaceae), *Ipomaea pes-caprae* (Convolvulaceae), *Mesembrianthemum acinaciforme*, *M. edule*, and other species of *Mesembrianthemum* (Aizoaceae); *Cynanchum* spp., *Schizoglossum euphorbioides* (Asclepiadaceae), *Canavalia* spp., *Tephrosia canescens* (Leguminosae), *Helichrysum teretifolium*, *Gazania uniflora*, *Berkheya maritima* (Compositae), *Passerina* spp. (Thymelaeaceae), *Samolus porosus* (Primulaceae), and *Salicornia* spp. (Chenopodiaceae).

The creeping forms grow in the shifting sand nearest to the sea; upright growing species at the margins of the coast-scrub. All tend to be fleshy and xerophytic and connect with the species of the dry climatic areas. While seashore hygrophilous forms may often be very ancient, the psammophilous halophytes, on the other hand, are apparently recent and derivative. The great majority belong to highly evolved floral types.

Guppy (1906, 1912, 1917) has dealt with such litoral plants

in great detail, especially with the dispersal of their seeds or fruits by ocean currents and other means.

Associated Plants of the Grass-Veld.—This is a huge assemblage of derivative forms adapted to open grassland conditions. They are nowhere dominant except in small patches in the grass-veld areas, but with increasing xerophytism they assume dominance in the transitional area between grass-veld and Karroo, and allied types are dominant in the Karroo itself. Ecologically they form either 'vernal aspect societies' or 'aestival and autumnal aspect societies.' The latter are more shrubby and tend to be transitional in the plant succession to scrub and forest. The vernal plants are most prominent in the early stages of the plant succession or when the succession is kept back by continual grass-burning. They flower and develop quickly in spring before the grass grows tall enough to shade them. They do not compete to any extent with the grasses, since, as a rule, they occupy deeper layers of soil. Competition with the grasses, however, is not altogether eliminated, for when the grasses remain unburnt for a succession of years the vernal aspect societies tend to become suppressed. A very large number of the associated plants are geophytes, and their bulbs, tubers, etc., may lie dormant in the soil for many years. Geophytes are very abundant among the Monocotyledons; in fact, as we have seen, Miss Sargent regards the geophilous tendency as accounting for the origin of the whole group. But underground storage of one kind or another is far more common than at first sight might be supposed among the Dicotyledons also. Sometimes the underground tubers reach enormous size, as in the Asclepiadaceae, but large, often much branched, woody or succulent underground rhizomes or short thick 'rootstocks,' sometimes combined with fleshy roots (see Figs. 25 and 27), are the rule rather than the exception in the other families of grass-veld plants as well. Sometimes, it is true, only the root system is involved, but usually at least the hypocotyl as well, if not the stem.

The autumnal aspect plants, however, branch freely above ground or become woody dwarf shrubs which often overtop the grasses and suppress them. In open spaces along roadsides or where the grass-veld has been brought into cultivation herbaceous ruderal species are found, and among these there is relatively a high proportion of annuals, few of which enter into the composition of stable grass-veld. Like the annual grasses, they become more prominent in the Karroo and drier regions of

the western side. They may be looked upon as the most recent

FIG. 24.—*Gazania longiscapa* DC.

$\frac{1}{3}$ nat. size. One of the earliest spring-flowering grass-veld plants in Natal.

types of all. It is interesting to note that some of the largest underground tubers belong to genera that phylogenetically are

often among the most primitive in each of the families to which they belong, e.g. *Raphionacme* among the Asclepiadaceae belongs to the primitive tribe Periploceae with loose pollen granules; *Elephantorhiza* among the Leguminosae belongs to the subfamily Mimosoideae, but probably this has little phylogenetic significance.

More important is the fact that many geophytic and other grass-veld genera are large and very widespread over the whole of South Africa, including the south-western region. According

FIG. 25.—*Gerbera kraussii* SCH. BIP.

½ nat. size. A common spring-flowering plant with well-developed fleshy roots.

to Willis' 'Age and Area Law' these would rank as relatively old. A few examples may be mentioned in the following families:

Liliaceae: *Anthericum, Chlorophytum, Urginea, Ornithogalum, Albuca.*

Amaryllidaceae: *Hypoxis, Nerine, Cyrtanthus.*

Iridaceae: *Moraea, Aristea, Hesperantha, Watsonia, Gladiolus.*

Orchidaceae: *Eulophia, Holothrix, Satyrium, Disa, Corycium, Disperis.*

Compositae: *Helichrysum, Felicia, Athanasia, Senecio, Ursinia, Berkheya.*

Leguminosae: *Lotononis, Argyrolobium, Indigofera, Lessertia, Rhynchosia.*

FIG. 26.—*Eulophia hians* SPRENGEL.
$\frac{1}{2}$ nat. size. Grass-veld orchid.

Sterculiaceae : *Hermannia.*

Asclepiadaceae : *Schizoglossum, Asclepias.*

Gentianaceae : *Sebaea.*

Scrophulariaceae : *Nemesia, Zalusianskya, Sutera, Melasma, Harveya.*

Selaginaceae : *Hebenstreitia, Selago.*

Thymelaeaceae : *Gnidia.*

Santalaceae : *Thesium.*

The widespread genera of grass-veld associated plants, however, are not necessarily large. Many of them consist of only one or two or a few species, e.g. *Buphane, Ammocharis, Curculigo, Penthea, Monsonia, Alchemilla, Seseli, Tripteris Dicoma, Matricaria,* and several others.

It is not so much the area covered by these widespread genera that is important as the fact that, though subordinate, non-dominant types, they have penetrated in such numbers through the temperate Fynbosch vegetation of the south-western region.

In the spring many grass-veld plants commence growth, even before the first rains, as soon as the temperature rises slightly, a fact which demonstrates that it is not in all cases the winter drought which causes the resting period in South African plants.

If the underground storage organs are more exposed to the heating effect of the sun, as, for instance, when the surface layers of soil are removed, renewal of growth is hastened. As soon as the first rains come all the vernal aspect plants shoot up very quickly, and in a week or two many have flowered. Others produce leafy stems first and flower rather later. The autumnal aspect plants grow more regularly and slowly and flower with the grasses. Many of the vernal species have a remarkably rapid rate of assimilation to begin with. They appear to perform most of the year's work before the grasses have grown to any size, but our information on this point is not based as yet on direct experimental data.

In many species, however, it can be observed that the size of the underground storage organs is astonishing, when one compares it with the very small aerial shoots. In some cases this may be explained by supposing that the perennial underground tubers, etc., are very old and have been added to year after year by the small aerial assimilating organs which are renewed annually. Here again there is room for more careful observations, measurements, and experiments over a period of years.

In autumn, as the dry anticyclonic conditions with lower temperatures again begin to prevail, the grass-veld plants, having

Fig. 27.—*Hypoxis rooperi* Moore.
½ nat. size. Common grass-veld geophyte.

shed their seed—with the exception of the Compositae, the majority have capsular fruits of one kind or another—begin to

wither and die back. If grass fires are prevented, some of them, protected by the covering of dead grass, remain green through the winter, at least near the ground. In other cases, the covering of dead grass seems to lead to a rotting of the aerial portions of the associated plants, and this may kill them out altogether. But grass fires are very nearly universal over the whole of the South African grass-veld, and this condition of things has gone on at least ever since man occupied the area. Grass fires, moreover, are not always caused by human agency. They may easily be caused by the frequent lightning discharges, and reliable information (published in one of the official Forestry Department's reports) has been received that boulders rolling down the rocky slopes and striking other rocks have set fire to bush or dry grass by friction. A grass fire once started may spread for hundreds of miles if the grass has not already been burnt in patches.

The dry aerial shoots of all the grass-veld plants are, therefore, regularly burnt off once a year, and fire must be reckoned an important factor in modifying, at least by its direct effects, the growth forms of the plants. Grass fires undoubtedly favour the continuance and spread of the vernal aspect societies, and, as already remarked, where grass fires are prevented, the majority of them tend to disappear. The autumnal aspect societies on the other hand and associated grass-veld plants generally, that are not geophytic but spend the winter with their shoots above ground, tend to be destroyed by the grass fires.

In minor details grass-veld plants vary much in their growth forms. Very frequently a rosette of leaves is produced just above the ground level with inflorescence axes arising from the centre. This type is very common among the Compositae. In other cases, the woody or tuberous underground 'rootstock' is crowned by a varying number of thin slightly woody or herbaceous aerial branches. Many grass-veld plants have fleshy or tuberous roots (see Figs. 25 and 27). The above belong partly Warming's class of Renascent herbs with multicipital rhizomes; but this class does not appear entirely satisfactory, for it is difficult to distinguish between herbs and suffrutices, and the majority would belong rather to his class 'Undershrubs of the Labiate type.'

Warming's class of Mat-geophytes is more definite and would include the numerous Monocotyledons which have corms, bulbs, or root tubers, and the Asclepiadaceae with perennial stem tubers. Travelling geophytes are more characteristic of vleis,

but they also occur in the grass-veld, e.g. *Hermannia* spp.

FIG. 28.—*Scilla lanceaefolia* BAKER
Very common grass-veld spring-flowering geophyte

and *Pteridium aquilinum*. Creeping plants are represented by various Cucurbitaceae, Passifloraceae, etc., but also to a smaller

degree by numerous others, e.g. *Rhynchosia* spp., *Hydrocotyle* spp., etc. Succulence is seen in *Crassula* spp., *Euphorbia* spp., etc., but these become much more prominent towards the Karroo. Almost every known type of xerophytic modification is seen among the thousands of species which we have estimated belong to this class. Of course, the grass-veld is by no means uniform. The grasses are not completely dominant over the whole of the great area covered by it. Everywhere there are rocky hill-sides, open spaces, moist spots, Kaffir pathways and roads, areas of scrub, of tree-veld, or of interspersed bush, and it is impossible to give a detailed ecological grouping of all the types of growth form met with. Our aim has been rather to deal with the main classes in detail, to note the chief characters of subordinate forms, and to put on record facts concerning any interesting or remarkable types in passing. Though the associated grass-veld plants vary so much in minor xerophytic characters, leaf shapes and arrangement of the leaves and branches, they all agree in the main growth-form characteristics that have been described.

CHAPTER IX

THE KARROO AND KARROID TYPES.—SEMI-DESERT AND DESERT TYPES OF THE WESTERN SIDE

The Karroo and Karroid Types.—We now come to the class of growth forms that are to be ranked as the most specialised and, on the whole, most recent in the South African flora. Our study of the associated grass-veld plants, and of the evolution of xerophytic grasses and of shrubs has formed a necessary introduction to a discussion of the Karroo types, since, as we have seen, the Karroo has derived most of its flora from the eastern and northern regions bordering on it. In many of the dry river-valleys of the eastern side there are conditions of xerophytism not far removed from those prevailing over the Karroo, and the vegetation responds in the same way. On the very dry slopes of the Tugela and Lower Mooi river-valleys in Natal there are many stony patches dominated by dwarf shrubs and succulents that have exactly the appearance of the Karroo, though the species differ.

The associated grass-veld plants in the mesophytic areas are entirely subordinate to the grasses. With increasing aridity, however, the former become more and more prominent. In the transitional areas between Karroo and grass-veld in the Karroid plateau, called ‘ Upper Region ’ by Bolus (1905) and ‘ Compositae Veld ’ by myself (1916)—though the name ‘ Compositae Steppe ’ was also used by Warming—various species of Compositae are more or less dominant mixed with *Aristida* spp. and other xerophytic grasses. The family Compositae in this area, according to Bolus, constitute 28 per cent. of the whole flora.

We have seen that in the grass-veld areas the associated plants belong, for the most part, to early stages of the plant succession and, except for the shrubby pieces that are transitional to forest, tend to be suppressed as succession advances. In the Karroo, it has been said, there is no plant succession, a statement which, in a sense, is true. The early colonising

stages in the Karroo remain the final stages. But the Karroo, as a whole, is closely related to and similar to the early stages of the plant succession over the whole of the eastern and northern grass-veld areas.

It is perhaps well, at this point, to elaborate somewhat an important point that has already been touched upon. In the mesophytic eastern areas the plant succession passes through a number of well-marked stages: A, *Aristida* spp. with abundance of associated plants; B, *Themeda* and *Andropogon* with fewer subordinate species; C, tambookie grasses with shrubs; D, scrub trees; E, forest. In the most favourable climatic areas the final stage E is reached, and, as we have shown, it is nearest to the ancient tropical forest type. With less favourable conditions the succession only advances as far as D. With increasing aridity it stops at C, or at B, or at A. In the Karroo it stops where it begins, though of course if minor features are taken into consideration there is a certain amount of successional development even in the Karroo.

The chief interest of these facts from our present standpoint lies in the connection between them and the general evolutionary history of growth forms. All the evidence from palaeontology, phylogeny, geographical distribution, and migration seems to point to the fact that ecological evolution has more or less exactly reversed the order of plant succession. Plant succession is towards the mesophytic; the evolution of plant growth forms has proceeded towards the xerophytic. In tropical forest the most ancient mesophytic-hygrophilous types remain, and it is unfortunate that we know so little regarding plant succession in the tropics. In the slightly drier subtropical areas the mesophytic climax types can only be established after the way has been prepared for them by more xerophytic types, *i.e.* by what we suppose are derivative types.

If the earliest types of Angiosperms arose in moist situations, the rest of the land surface must have been left still dominated by Gymnosperms. Gradually more and more xerophytic types of Angiosperms were evolved. Many of them, of course, may be ancient enough to occur amongst our earliest known fossils. As soon as these had conquered a place for themselves in drier habitats, an opportunity was given through the workings of the laws of plant succession for the more ancient, more mesophytic or hygrophilous forms to extend their distribution. The process was continued. New pioneer forms were evolved to prepare the way for the further extension of the Angiospermous

type. With the evolution of the grasses a tremendous step forward was made. Vast areas were in the course of time completely dominated by this new growth form.

There were some areas, however, too dry for the grasses. Plastic as they are in their requirements, highly differentiated as they became, they failed to cover the whole range of climates. The physiological anatomy of the Angiospermous type in other families, however, gradually met the demands on it, partly by the device of establishing a large water-balance as in the succulents, partly by increased lignification in the assimilating organs, and by numerous other devices.

The full analysis of all the various steps is a task to which botanists and plant physiologists will probably continue to devote increased attention. The Gymnosperms had never managed all this so successfully, though our *Welwitschia mirabilis*, lingering on in its desert habitat, shows us something of what they did accomplish. *Welwitschia*, as is well known, is a very slow-growing plant. To restrict water loss and, at the same time, restrict assimilation and rate of growth is not very difficult. The really difficult task for any plant is to grow as rapidly as possible with a minimum water-supply at its disposal. Rapid growth means success in competition. The taller-growing plants suppress the others. The important thing that should be measured for all plants is not their transpiration rates or total water loss, but their 'water requirements,' *i.e.* the ratio of water utilised to dry material formed.

To take in carbon dioxide and, at the same time, prevent excessive loss of water vapour through the same openings—the stomata—must always be difficult, unless it were possible to make the passage of gases inward into the leaf tissues easier than the passage of gases outward.

Many of the Angiosperms of the Karroo and drier parts of South Africa have succeeded in restricting their 'water requirements' to a remarkable extent. Dr. Marloth has pointed out to me that among all the weird growth forms of Karroo plants with which he is familiar, some of the species of *Eriospermum* are most interesting. They build up large underground tubers with the help of a single leaf which is often reduced to a mere thread. In his works 'Das Kapland' and 'Flora of South Africa' Marloth has illustrated many other growth forms of Karroo plants and he has also devoted much attention to the boundaries between the south-western region and the Karroo. The 'Sketch of the Floral Regions of South Africa,' by Bolus,

one of the pioneer works on plant distribution in South Africa, remains very valuable, though the details are not, of course, up to date. The following general account of the Karroo and Karroid vegetation is largely based on the works of these two authors, supplemented, as far as possible, by personal observations.

In the transitional region, as well as in the Karroo proper, the Compositae are the most important family. The genus *Pentzia*, though not the largest, is one of the most important, including, besides other species, *Pentzia virgata*, the Karroo bush, which is often dominant. *Pteronia* is a much larger genus with between 30 and 40 Karroo species. *Pteronia pallens* (the Witbossie) is one of the commonest. There are over 20 species of *Senecio* (not including the sect. *Kleinia*) and about 16 species of *Helichrysum* in the Karroo proper, but these genera increase greatly in importance in the transitional belt. The figures given by Bolus—86 species for *Senecio* and 71 for *Helichrysum*—are complicated by the fact that he included the bordering mountains, which in some cases have a south-western flora. Other important genera of Compositae are *Nestlera*, *Relhania*, *Chrysocoma* (*C. tenuifolia* is abundant), *Eriocephalus*, *Felicia*, *Othonna*, *Sphenogyne*, *Cenia*, *Berkheya*, *Dicoma*, *Doria*, *Euryops*, and *Osteospermum*. The sect. *Kleinia* and some other species of *Senecio* are succulent, but the majority of the Compositae are dwarf shrubs, suffrutices or herbs, and a few are annuals (species of *Helichrysum*, *Senecio*, *Cenia*, and *Sphenogyne*). The Aizoaceae are peculiarly characteristic of this region. The genera *Pharnaceum*, *Hypertelis*, *Psammotropha*, *Adenogramma*, *Glinus*, *Orygia*, *Mollugo*, *Limeum*, and *Giesekia* are small suffrutices or herbs, often annual. Species of *Galenia* and *Acrosanthes* are usually dwarf shrubs. *Galenia africana* (the Kraal Bosch) is often subdominant or dominant over patches. The succulent tendency is seen in *Tetragonia*, *Aizoon*, and culminates in the huge genus *Mesembrianthemum*, which represents the highest floral as well as ecological development in the family; indeed, in many respects it represents the highest specialisation in the whole South African flora. In general it has solved the difficulty of existence under arid conditions by its succulence, but the species *M. spinosum* is spiny as well and is dominant over much of the very driest parts of the Karroo.

The species which have come to look exactly like the stones among which they grow (some of them occurring in the western region), first described by Marloth, have given rise to much

discussion on the question of 'Plant Mimicry.' *M. canum, M. calcareum, M. bolusii, M. simulans, M. hookeri* are examples. The species *M. rhopalophyllum* has its green assimilating parts below ground and admits light to them by a convex 'window' level with the soil surface. It is illustrated by Marloth (1913, Plate 52) and constitutes another of the 'freaks and marvels' of the Vegetable Kingdom. *M. hookeri, M. pseudotruncatellum, M. opticum,* Marloth states, are similar. The Crassulaceae, as represented in the Karroo, are highly evolved types both floristically and ecologically in the direction of succulence. The genus *Crassula* is the largest with at least sixty species of leaf succulents. *Cotyledon* species are larger, more conspicuous types of stem succulents. The amount of detailed variation in the growth forms of the Crassulaceae are well illustrated by Marloth in 'Das Kapland,' where photographs of *Crassula perfossa, C. pyramidalis, C. barbata, C. haemisphaerica, C. columnaris,* and *Cotyledonreticulata* are reproduced. *Cotyledon fascicularis* is one of the commonest species on Karroo hillsides.

FIG. 29.—*Hoodia bainii* DYER.
½ nat. size.

The Asclepiadaceae have already been noted as very important geophytic dicotyledonous associated plants of the grassveld and as succulent climbers in eastern scrub. As in the

Aizoaceae and Crassulaceae, the highest floristic as well as ecological types are found in the Karroo. These belong to the section Stapelieae and according to the 'Flora Capensis' include the following numbers of species: *Pectinaria* (5), *Caralluma* (23), *Trichocaulon* (11), *Hoodia* (7), *Tavaresia barklyi*, *Huernia* (23), *Diplocyatha ciliata*, *Stapelia* (cir. 70), *Piaranthus* (11), *Duvalia* (14), or a total of about 160, some of them purely western. Some of the eastern genera belonging to other sections of the family have outlying species in the Karroo. Species of *Hoodia* and *Trichocaulon*, in addition to being succulent, have spines or stout bristles. The genus *Euphorbia* is important in all the drier parts of South Africa. In the Karroo the following are some of the commonest species: *E. coerulescens* (often dominant), *E. mauritanica*, *E. stellaespina*, *E. enopla*, *E. tenax*, *E. rhombifolia*, *E. caterviflora*, *E. mundii*, *E. fusca*, *E. crassipes*, *E. multiceps*, *E. ferox*, *E. horrida*, *E. dregeana*, and several others.

Another important leaf succulent genus is *Anacampseros* (Portulacaceae), of which there are about a dozen Karroo species. The leaves are sometimes very small. The genus *Oxalis*, according to Bolus, has over 30 Karroo species. The Zygophyllaceae include *Augea capensis* and *Sisyndite spartea*, both important species, especially towards the western side, as well as species of *Zygophyllum*. The Leguminosae, though so well represented in the grass-veld regions, in the Karroo, according to Bolus' statistics, is only about as important as the Aizoaceae. *Indigofera* is the largest genus with over 20 species. Among the Geraniaceae the genus *Pelargonium* has over 40 Karroo species, many of them characteristic, with large swollen succulent stems, e.g. *P. carnosum*, *P. crithmifolium*, and *P. munitum*, illustrated by Marloth in the work already cited. *Sarcocaulon patersoni* and other species are found towards the west. In the Selaginaceae the genera *Walafrida* and *Selago* are important. *Lycium* spp. (Solanaceae) are usually spiny, and of the 18 described in the 'Flora Capensis' 15 occur in the central region, though they are not all confined to it. Several of them are also characteristic of the dry valley-scrub of the eastern side. Many other scrub species also extend into the Karroo region, especially on the hills and kopjes, e.g. *Portulacaria afra*, *Rhus* spp., *Capparis oleoides*, *Rhigozum trichotomum*, *Carissa arduina*, *Aloe ferox* and other *Aloe* spp., and *Encephalartos* spp. On many of the Karroo hillsides the shrubby *Salsola aphylla*, the Ganna bush, is dominant; in brak places *Tamarix articulata* is abundant and

widespread. In the little Karroo, Marloth describes a 'Guarri formation' dominated by the Guarri or Gwali, *Euclea undulata*. Other Karroo shrubs and trees, including the widely extended stream- and river-bank species, were dealt with in earlier chapters.

Among the Monocotyledons the geophytic families Liliaceae, Amaryllidaceae, and Iridaceae have proved themselves well adapted to Karroo conditions, but the Orchids, except in the transitional regions, are very rare or absent. Bolus places the Liliaceae as fourth, the Iridaceae as eighth, and the Amaryllidaceae as fourteenth in order of importance among families of Karroo plants numerically. *Ornithogalum* is the largest genus though not the most characteristic. *Buphane disticha* is one of the commonest species. Other important bulbous or tuberous geophytic genera are *Eriospermum*, *Bulbine*, *Anthericum*, *Massonia*, *Polyxena*, *Androcymbium*, *Gethyllis*, *Brunsvigia*, *Haemanthus*, *Moraea*, *Romulea*, *Hesperantha*, *Lapeyrousia*, and *Babiana*. The genus *Aloe* is of a distinct growth-form type. Besides eastern scrub species already referred to, the following are important Karroo species: *Aloe microstigma*, *A. aristata*, *A. longistyla*, *A. striata*. There are also many similar fleshy-leaved species of *Haworthia*, *Gasteria*, and *Apicra*, e.g. *Haworthia viscosa*, *H. altilinea*, *H. venosa*, *H. laetevirens*, *H. bolusii*, *H. margaritifera*, *Gasteria disticha*, *Apicra deltoidea*.

Another distinctive liliaceous growth-form type is the genus *Asparagus*, of which there are a number of Karroo species, e.g. *Asparagus microraphis*, *A. burchelli*, *A. stipulaceus*, *A. africanus*, *A. striatus*, *A. racemosus*, *A. sarmentosus*, *A. medioloides*.

The close connections between the Karoo flora and the eastern and northern are perfectly clear from the above enumeration of the dominant and characteristic genera and species. On the other hand, the Karroo flora is very distinct from the south-western, which bounds it on the other side and to a certain extent surrounds it on the mountains. Marloth's investigations have shown that the boundary lines between Karroo and south-western vegetation are usually remarkably distinct. There is very little mixing of the two elements and the transition is not gradual, though in places the Karroo flora seems to be gaining on the south-western. Nevertheless, some of the Karroo types have succeeded in invading the south-western area, even as far as the Cape Peninsula. These will be referred to again in the next chapter.

The growth forms of Karroo plants show the following features:

1. On the rocky hillsides various shrubs and small trees occur, all with eastern affinities. They are xerophytic forms similar to those occurring in dry-valley scrub and exhibit the same evolutionary features: decrease in size, increased branching, decrease in size of the leaves, leaves compound (*e.g.* in species of *Rhus*), spinosity in *Lycium* spp. and many others, succulence (*Aloe* spp., *Euphorbia* spp., *Cotyledon fascicularis*, *Portulacaria afra*, etc.), and many minor xerophytic characters.

FIG. 30.—*Aloe ferox* MILLER. Much reduced.

2. Along the river-banks and in dry river-beds trees and shrubs reach a somewhat larger size but exhibit the same xerophytic characters. Examples: *Acacia karroo* (sometimes with *Viscum rotundifolium* parasitic on it), *A. giraffae* (along the Orange river), *Salix capensis*, *Rhus lancea*, *Rhus viminalis*, *Zizyphus mucronata*, *Royena* spp., *Combretum erythrophyllum*.

3. On the plains the dwarf-shrub type is dominant, e.g. *Pentzia virgata* and other Compositae, *Galenia*, *Walafrida*, etc. They are similar to associated grass-veld plants but much more xerophytic, often somewhat heath-like in general appearance, with small leaves. The visitor to the Karroo is, first of all, struck by the almost total absence of green colour. Everywhere there are various shades of greys and browns, but hardly ever any green.

4. Thorn development is common, though not among the Compositae. *Lycium* spp., *Asparagus* spp., *Mesembrianthemum spinosum*, and many of the succulents show it. Often it is developed to an extreme degree.

5. Succulence is one of the most common features of Karroo plants. It is shown by the Crassulaceae, Asclepiadaceae, *Pelargonium*, *Euphorbia*, *Senecio*, *Mesembrianthemum*, and many others.

6. The geophytic type of growth form is, in some respects, allied to the succulent, since the underground tubers and bulbs store water as well as food. It may be associated with succulence in the aerial parts as well. Monocotyledonous geophytes are common in the Karroo, but many of the dicotyledons also have underground storage. Often the aerial assimilating organs are relatively very small as compared with the large underground storage organs, *e.g.* in *Eriospermum* spp.

7. Annuals, or Ephemerals, represent the most perfect kind of adaptation to dry conditions. They occur among the Compositae (species of *Arctotis*, *Helichrysum*, *Senecio*, *Sphenogyne*, *Cenia*), among the Scrophulariaceae (species of *Manulea*, *Sutera*, *Phyllopodium*, *Nemesia*), among the Gramineae, as already described, and in many other families as well.

The annuals in the Karroo form a large part of the ‘ opslag ’ type of vegetation which springs up and flowers immediately after rains. It forms seed quickly and then withers and dies. In the form of seed the species can survive long periods of extreme drought. Some of the ‘ opslag ’ vegetation consists of perennials which retreat during periods of drought to the moister centres of distribution.

Annual weeds also occur as ruderals in cultivated land, but little of the Karroo is cultivated except such parts as can be irrigated. The Rhenosterbosch (*Elytropappus rhinocerotis*), a perennial Composite, which seems to be generally assisted in its spread as a result of man's interference, is becoming increasingly abundant in parts of the Karroo. The Prickly Pear (*Opuntia*) is a pest in other parts, but it is not our present purpose to deal with general ecology or introduced species.

Though the Angiosperms are completely dominant in the Karroo and drier parts of South Africa at the present time, the presence of *Encephalartos* on some of the eastern Karroo hillsides and the presence of various xerophytic ferns (e.g. *Pellaea auriculata*, *Cheilanthes pteroides*, *Ch. induta*) give us

a hint as to the possible state of affairs in dry continental areas before the rise of the Angiosperms.

The growth forms of Karroo plants have been evolved chiefly in response to the dry climatic conditions, but it should be noted in passing that a dry climate not only affects plants directly but it also changes the soil conditions. Karroo soils are very rich; indeed, salts often accumulate in them to such an extent that they become brackish and the vegetation halophytic, as when *Tamarix* becomes dominant. The distribution of many of the species is no doubt influenced by variations in soil conditions. *Acacia* spp. are generally believed to favour soils rich in lime, but it may be that they react in the first place to climate. Soils of drier climatic areas are often richer in lime as in other salts.

The vegetation of various types of 'pan' should also be studied from this standpoint. They are caused, in the first place, by wind erosion, but in all the drier parts of the country they have come to be salt pans, with *Tamarix articulata*, *Salsola* spp., *Atriplex halimus*, *Lycium* spp., *Statice* spp., and other halophytes.

Semi-Desert and Desert Types of the Western Side.—Some botanists might be inclined to classify all the Karroo as semi-desert or even as desert. It corresponds very closely, for instance, to the Arizona 'deserts' of North America. Such a term, however, would hardly appeal to the Karroo farmer. A region clothed with succulents and dwarf shrubs, with the rich soil accompanying semi-arid conditions, with a corresponding high feeding-value in its natural vegetation, with water usually to be obtained from wells at a moderate depth, capable of supporting large numbers of domestic animals, particularly sheep, cannot, if we use words in their commonly accepted sense, be called desert. No word in common use should be used ecologically with a meaning different from the usual, and certainly the term 'desert' is not applied to the Karroo in South Africa. The term 'Gouph,' or 'The Gouph' (a Hottentot word meaning 'empty,' 'bald,' 'naked,' or 'nothing'), is applied to the driest parts of the Karroo around Matjesfontein. The name 'Karroo' with the adjective 'Karroid' are useful ecological descriptive terms, now generally applied in South Africa, but their use might with advantage be extended to other countries where semi-arid regions are dominated by dwarf shrubs and succulents.

Towards the western side, however, there are stretches

where real desert conditions prevail. This does not include the so-called Kalahari desert, which is pure grass-veld (sand-veld) with a rainfall up to 20 inches in the year, supporting great herds of antelope and other game. The absence of surface water owing to the sand covering was probably the reason why early travellers named the Kalahari a desert. Succulent fruits, bulbs, etc., seem to supply all the water needed by the various antelopes, etc., that inhabit the region.

The most extreme desert conditions of South Africa are on the western litoral strip, the Namib, where plants are few and far between. Pearson (1911) states that on one occasion he rode for a distance of four kilometres without seeing any.

From such extreme desert conditions as this to the Karroo type, there are all gradations. Much of the Western Cape is pure Karroo. The Kamiesberg mountain range, as explained in the introductory chapter, has a fairly high rainfall and still more mesophytic vegetation. The Richtersveld, on the other hand, is very dry. The whole region is still only partially explored botanically, though Pearson's expeditions added much to our knowledge, and the work of Schinz, Range, Pole Evans, Marloth, and others on the South-West Protectorate flora north of the Orange river has made the flora fairly well known, at least from the systematic standpoint. Various published lists show that while the species of the western side are often, and the genera sometimes, endemic, while certain families, *e.g.* Amarantaceae, Scrophulariaceae, Zygophyllaceae, are unexpectedly prominent, yet, on the whole, the flora is surprisingly similar to that of the eastern side.

The vegetation of the rocky hillsides differs from that of the stony or sandy plains in the Karroo. The watercourses are usually dry and often have the thorny type of scrub described for the Karroo. Often the river-beds are sandy. Looking through Pearson's lists of plants collected, one notices that almost half of the locality records are given as sandy, or occasionally stony, river-beds.

The effect of semi-desert or desert conditions on the vegetation may be summed up very briefly :

(1) There is a vast reduction in the number of individual plants.

(2) There is a reduction also in the number of species.

(3) The perennials are the most extreme types of xerophyte, usually either thorny or succulent or both.

(4) There is a high proportion of annuals in the flora, short-

lived mesophytes that last only for a few weeks after rain has fallen and spend the long dry intervals in the form of seed.

There appears to be a very distinct tendency on the part of the annuals to cluster round the scattered bushes of perennials. Apparently even under semi-desert or desert conditions plant succession plays a part, or at least there is a certain amount of development, even in such very open types of plant community. Often the perennials are killed by the long periods of drought, yet after rains the annuals appear in isolated clusters marking the spots where the perennials have been.

It is not possible to give more than a very general picture of the composition of the scattered types of plant community and commoner genera and species of the west. The genus *Euphorbia* is well represented. *E. gummifera*, *E. cervicornis*, *E. virosa*, *E. frutescens*, *E. namibensis*, *E. guerichiana*, *E. brachiata*, *E. lignosa*, *E. cibdela*, *E. spartaria*, *E. ephedroides*, *E. mauritania*, *E. dregeana*, *E. gregaria*, and *E. gariepina* are some of the species recorded, but there are several others. All these are succulent.

Another large succulent genus is *Mesembrianthemum*, of which about eighty species are listed by Pearson. Most of his records for the various species are either stony or sandy plains. The Aizoaceae are also represented by species of *Tetragonia*, *Anisostigma*, *Aizoon*, *Galenia*, *Trianthema*, *Orygia*, *Mollugo*, *Pharnaceum*, *Giesekia*, *Semonvillea*, and *Limeum*. The Zygophyllaceae have the two species *Sisyndite spartea* and *Augea capensis*, both of which are abundant and very widespread, and in addition about twenty species of *Zygophyllum*, an important western and Karroo genus, and four species of *Tribulus*. The Asclepiadaceae have *Microloma* spp., *Cynanchum* spp., *Ectadium* spp., *Sarcostemma viminale*, *Pergularia gariepensis*, the very common *Hoodia gordoni*, and several others. The Cucurbitaceae are rather prominent as stragglers over the sand, e.g. *Trochomeria debilis*, *Cucumis africana*, *C. rigidus* and other species, *Kedrostis punctulata*, and about half-a-dozen species each of *Corallocarpus* and *Coccinea*. The common Water Melon (*Citrullus vulgaris*) is one of the most important fruits in all the drier parts, including the Karroo. *Acanthosicyos horrida* is one of the few plants found in the Namib.

The Geraniaceae includes *Sarcocaulon burmanni* (Bushman's Candle), with several other species of the same genus and about thirty species of *Pelargonium*. *Monsonia* spp. are found in

moister spots. *Hermannia* (Sterculiaceae) is prominent in the west as it is in eastern grass-veld. *Talinum africanum* (Portulacaceae) is common and widespread on the sandy plains. The family also includes several species each of *Anacampseros* and *Ceraria*. The Crassulaceae are, as is to be expected, well represented by about thirty species of *Crassula* and a dozen species of *Cotyledon*, all succulent.

In the Capparidaceae there is the fleshy, almost leafless, *Cadaba juncea*, *Boscia foetida*, a species of *Capparis*, two species of *Maerua*, the herbaceous *Cleome minima*, *Gynandropsis pentaphylla*, and four species of *Polanisia*. The Anacardiaceae have many species of *Rhus* and several of *Heeria*.

The Scrophulariaceae are rather well represented and include numerous annual plants. The most important genera are *Aptosimum*, *Peliostomum*, *Anticharis*, *Diascia*, *Nemesia*, *Manulea*, and *Sutera*. In the Solanaceae there are numerous species of *Lycium* and a few species of *Solanum*.

Among the Compositae many of the genera already dealt with for the Karroo are represented. A glance through Harvey's arrangement of the genus *Senecio* in the 'Flora Capensis' will show how predominantly western is the whole section 'Annui.' These were mostly collected by Drège.

The Acanthaceae have species of *Ruellia*, *Petalidium*, *Blepharis*, *Acanthopsis*, *Barleria*, and *Monechma*. The Leguminosae are fairly well represented, the largest genera being *Lotononis*, *Lebeckia*, and *Indigofera*, while *Acacia* spp. and *Parkinsonia africana* are the most prominent, especially along the dry river-courses. *Oxalis* is represented by about a dozen species. The Amarantaceae have the following genera: *Hermbstaedtia*, *Aerva*, *Sericocoma*, *Sericocomopsis*, *Sericorema*, *Marcellia*, *Arthraerua*, *Leucosphaera*.

The Chenopodiaceae are usually halophilous, including species of *Atriplex*, *Salsola*, and *Suaeda fruticosa*, *Salsola zeyheri* and *Salsola aphylla*, the widespread Ganna Bush.

The Bignoniaceae have two very important species, *Catophractes alexandri* and *Rhigozum trichotomum*, the latter (the Driedoorn) often the most common plant over wide areas.

Perhaps the most striking plant of all is the Kokerboom (*Aloe dichotoma*), widespread and common, especially on rocky outcrops.

This enumeration, as in the case of the Karroo, must not be considered by any means exhaustive, but on the whole it can be taken as representative. It shows how predominantly

succulent the whole desert flora of the west has become. The grasses, species of *Aristida*, *Eragrostis*, *Enneapogon*, etc., have already been dealt with. To conclude the picture I cannot do better than quote Pole Evans' (1920) account of the Namib, which is the most extreme west litoral desert type.

'Some five distinct zones of vegetation may be distinguished, viz. that of the western slopes of the Escarpment, the Gravel Plains, the Sandy Dunes, the Rocky Hills, and the Seashore.

'On the rocky slopes of the Escarpment, the Kokerboom (*Aloe dichotoma*), *Euphorbia virosa* and *E. dregeana* are most conspicuous, whilst among the foothills clumps of *Euphorbia brachiata* are common, and associated with them are plants of the Bushman's Candle (*Sarcocaulon burmanni*) and *Pelargonium crassicaule*, *Augea capensis*, *Mesembrianthemum micranthum*, *Galenia africana*, and *Euphorbia namibensis*.

'Below this the vast gravel plains are for miles and miles almost destitute of vegetation or support a scanty growth of Vogelstruis grass (*Eragrostis spinosa*). In some places the only plant on these plains is an annual *Mesembrianthemum*; on others nothing but lichen growth covers the small pebbles. Towards the north only a few isolated plants of *Aerva desertorum* occur over vast stretches, while *Welwitschia mirabilis* is found in a few localities and is usually associated with *Zygophyllum stapfii*.

'The sand dunes support a very scanty vegetation which is made up chiefly of scanty tufts of Vogelstruis grass (*Eragrostis spinosa*), *Eragrostis cyperoides*, the Ganna Bush, *Salsola zeyheri*, *Statice scabra*, and *Mesembrianthemum marlothii*.

'On the rocky hills fringing the seashore the vegetation is more varied and is composed of many extremely interesting forms such as *Mesembrianthemum opticum*, *M. saxetanum*, *M. rhopalophyllum*, *Trichocaulon cactiforme*, and *Euphorbia lignosa*; other common plants are *Ectadium virgatum*, *Eremothamnus marlothianus*, *Dicoma tomentosa*, *Pituranthus aphyllus*, *Augea capensis*, and *Lebeckia multiflora*.

'On the seashore three plants are fairly common, viz. *Salsola zeyheri*, *Chenolea diffusa*, and *Salicornia natalensis*. The river-valleys which traverse the Namib carry a very typical vegetation. In the upper reaches of the valleys, especially in the north, considerable tree-growth occurs; in the dry river-beds the characteristic trees are the Anaboom (*Acacia albida*), the Camel Thorn (*Acacia giraffae*), the Omumborumbonga

(*Combretum primigenum*), the Cape Ebony (*Euclea pseudebenus*), the Tamarisk (*Tamarix articulata*), and the Choris (*Salvadora persica*).

'The low-lying valleys are practically dominated by vast stretches of nothing but the Aggenys Euphorbia (*E. gregaria*).

'Nearer the coast, where several of the rivers disappear under the sand dunes, their underground courses can frequently be detected by the presence of the Naras (*Acanthosicyos horrida*) and the Tamarisk (*Tamarix articulata*) amongst the dunes.'

CHAPTER X

THE TEMPERATE OR MOUNTAIN AND SOUTH-WESTERN FLORA

Theories regarding the possible origin of this element of the South African flora and its general distribution and relationship to the tropical-subtropical element have already been discussed. The region occupied by it even in the south-west is very mountainous, and its extensions northwards are almost entirely on the mountains. On the western side it has an 'outlier' on the Kamiesberg and, as already explained, it extends eastward along the mountains of the Karroo region, the Zwarteberg, Witteberg, etc. On the Stormberg and Drakensberg it tends to mix to a greater extent with the eastern flora. In the areas where it meets with the Karroo flora, the mixing is much less evident.

The surprising thing is that, intimately connected as the two elements of the South African flora are geographically and that for a long period of time, the mixing is not greater. The different climatic conditions (winter rains and dry summers) in the south-west doubtless help to explain why the flora remains so distinct. It is different ecologically as well as in its origin.

The evidence from phylogeny, already summarised, indicates to a certain extent at least that the south-western flora is a very old one, older than the Karroo flora and other derivative South African subtropical types, but probably not older than the tropical. In this connection, the results of Dr. Marloth's studies in the transitional belt between the Karroo and the south-western region are interesting. They seem to indicate that, at the present day, the Karroo flora is aggressive and is tending gradually to invade the region hitherto occupied by the south-western vegetation.

This is apart from the Karroo genera and species which have actually penetrated right through the south-west. These, it may be claimed, are counterbalanced by south-western genera and species that have succeeded in penetrating equally far

through the eastern subtropical grass-veld, even to the coast-belt of Natal.

The woody types of growth form, though often much dwarfed and stunted, are completely dominant in the mountain and south-western flora, and this favours the view that it is a fairly ancient type. Associated with the dominant shrubs there are many derivative growth forms. The evidence from phylogeny would support the view that in many families even these are relatively ancient as compared with similar types in the eastern subtropical flora, *e.g.* in the Iridaceae. As already pointed out, among the subordinate associated plants the genera are often very widespread over the whole of South Africa. Many of the larger genera, e.g. *Helichrysum*, *Senecio*, *Disa*, *Anthericum*, *Ornithogalum*, are about equally as well represented in Natal as in the Cape Peninsula.

The south-western flora may have occupied a much wider area at one time, and Marloth's observations would support this view. It is interesting to speculate what the flora of the whole eastern side may have been before the present subtropical types were evolved to take possession of it. Was it all gymnospermous ? or may there have been an earlier Angiospermous flora that has now disappeared ? If the latter alternative is correct may the former eastern flora have been similar to the present south-western ?

The speculation is rather an idle one, for at present it is quite impossible to decide.

Though the south-western flora may now be more restricted in its distribution than formerly, nevertheless it must not be looked upon altogether as a decadent flora. The enormous variety of endemic forms and the high amount of general differentiation, the large size of many of the genera and the penetration of many genera and species through eastern grass-veld—itself a derivative type—are against this view. Among one of the most characteristic south-western families, the Proteaceae, there are genera like *Faurea* and many species of *Protea* that are common or dominant in subtropical tree-veld. Other south-western families also have outliers that have proved themselves successful in competition with the subtropical flora, as will be noted below.

While some of the elements of the south-western flora appear to be old, it is impossible to say whether the whole of this flora is to be considered old or even relatively old. The predominance of such families as the Compositae and Ericaceae hardly

favours such a view. Even such a family as the Proteaceae show advance in certain respects. Like so much else connected with the South African flora, the subject of the origin and relationships of the temperate element is very alluring but very difficult.

In the south-western region, while Fynbosch or Macchia shrubs cover nearly the whole area in the climax stages of succession, there are some fairly large areas, as at Knysna, where the climax type is eastern forest. Patches of similar forest, much reduced in numbers of component species, occur even as far as the Cape Peninsula.

At Knysna the Fynbosch shrub *Virgilia capensis* (the Keurboom) forms large transitional associes which prepare the way for the development and extension of the forest. The following is the composition of the Knysna forest modified very slightly from that given by Marloth in 'Das Kapland': *Podocarpus falcata* (*P. elongata*), *P. latifolia*, *Olea laurifolia*, *Pterocelastrus variabilis*, *Curtisia faginea*, *Apodytes dimidiata*, *Platylophus trifoliatus*, *Ocotea bullata*, *Elaeodendron croceum*, *Nuxia floribunda*, *Ilex mitis*, *Rapanea melanophleos*, *Cunonia capensis*, *Olinia cymosa*, *Ekebergia capensis*, *Calodendron capense*. All the above are trees reaching a height of 15 metres or more. The following are smaller trees or shrubs: *Gonioma kamassi*, *Olea foveolata*, *Halleria lucida*, *Plectronia obovata*, *P. mundii*, *Royena lucida*, *Gymnosporia acuminata*, *G. peduncularis*, *Lachnostylis hirta*, *Ochna arborea*, *Kiggelaria dregeana*, *Virgilia capensis*, *Celtis kraussiana*, *Euclea lanceolata*, *Buddleia salviaefolia*, *Burchellia capensis*, *Gardenia rothmannia*, *Trimeria grandifolia*, *Trichocladus crinitus*.

Comparison with the mesophytic eastern forest described in Chapter IV will show that this large Knysna forest is simply an outlier of the eastern type within the south-western region. It is intimately connected with the south-western vegetation which it replaces in the course of the plant succession. Some of the eastern genera or species of trees and shrubs allied to or identical with those occurring in scrub and tree-veld mix still more intimately with the Fynbosch, especially species of Rhus, e.g. *Rhus rosmarinifolia*, *Rh. stenophylla*, *Rh. angustifolia*, *Rh. tomentosa*, *Rh. villosa*, *Rh. pyroides*, *Rh. mucronata*, *Rh. dregeana*, *Rh. glauca*, *Rh. lucida*, *Rh. scytophylla*, *Rh. undulata*.

In addition the following are important: *Ilex mitis* (near water), *Gymnosporia buxifolia*, *G. lucida*, *Olea verrucosa*, *Olea capensis*, *Halleria lucida*, *H. elliptica*, *Royena lucida*, *Royena*

glabra, *Cussonia thyrsiflora*, *Melianthus major*, *Osyris abyssinica*, *Sparmannia africana*.

Of the typically south-western genera, with the exception of the Silver Tree (*Leucadendron argenteum*) hardly any reach tree size. On the Cedar Berg mountains the gymnospermous Clanwilliam Cedar (*Widdringtonia juniperoides*) is common, representing the remnants of a still older type. It is interesting to find that all the taller trees and shrubs with growth forms nearest to the ancient tropical type occurring in the south-west have eastern affinities or indeed are mostly eastern species.

It does not follow, of course, that in the south-west they are necessarily ancient. Even the highly specialised Karroo flora has penetrated to a certain extent through the region. The stem succulent *Cotyledon fascicularis* is very prominent on many south-western hillsides. Species of *Crassula* and *Mesembrianthemum* are abundant and widespread. There are even a few succulent Euphorbias. Marloth, from Bolus and Wolley-Dod's list for the Cape Peninsula alone, summarises the succulents in numbers of species as follows: *Pelargonium* (2), *Crassula* (29), *Rochea* (4), *Cotyledon* (5), *Mesembrianthemum* (62), *Tetragonia* (6), *Kleinia* (2), *Othonna* (13), *Stapelia* (1), *Euphorbia* (3), *Aloe* (3), making a total of 130 out of 2119, or about 6 per cent.

The mountain and south-western vegetation, though dominated by sclerophyllous shrubs, is not composed entirely of this one class of growth forms. There is almost as great diversity as in the tropical-subtropical regions, though it has been found convenient to deal with the vegetation of the region as a whole, since other types of growth form are subordinate. There are no grassland areas, and the numerous grasses occur sparsely scattered in tufts among the dominant shrubs.

The true Macchia may be from ten to twenty feet in height, or, in the case of some of its component species, even higher.

Below this, there is every gradation down to a low type of Heath, with such species as *Blaeria ericoides* dominant. It is similar in many respects to the *Calluna* of Europe. Over large areas, especially where the Veld has been interfered with, the Rhenosterbosch (*Elytropappus rhinocerotis*) is completely dominant. It is also a heath-like shrub, though it belongs to the Compositae.

The heath types often form a stage in the plant succession to the climax Macchia, just as the latter often gives way to forest. All over the region there are subordinate types of

growth form, water plants, marsh plants, geophytic plants, climbing plants, psammophilous and halophytic plants, annuals, etc., but to a certain extent these have already been dealt with for the purposes of comparison with the tropical-subtropical flora.

In the account which follows attention is directed first of all and chiefly to the dominant sclerophyllous shrubs.

Among the Ericaceae the huge genus *Erica* is the most important with about 480 African species, mostly south-western. A few species extend eastward and northward through the tropics, including *Erica arborea* on the mountains of East Central Africa. Twenty-three species are recorded for Natal, of which two or three descend to the coast-belt, but the majority are confined to the mountain ranges, where they are prominent. Other genera with eastern extensions are *Philippia*, *Blaeria*, and *Ericinella*.

While the Ericaceae are common in Europe, Asia, and North and South America, they are almost absent from Australasia, where they are replaced by the nearly allied Epacridaceae. In tropical regions they occur at higher altitudes, but have there in *Erica arborea* retained the more ancient tree growth form, as also in the Asiatic Rhododendrons. The fact that the Australian Epacridaceae (which differ chiefly in the stamens) are ranked as a separate family may possibly indicate that the South African Ericaceae have been evolved since the connections with Australia—if these ever existed—were broken.

Among the South African Proteaceae one genus, *Faurea*, which reaches tree size, has 15 species and is purely subtropical and south-east African. It is prominent in the Brachystegia tree-veld of southern Rhodesia, and one species, *Faurea saligna*, is often completely dominant on sandy soil in one or two localities in Natal.

The genus *Protea* (130 species) is mostly south-western. Some of the Sugar-bushes, e.g. *Protea mellifera*, *P. grandiflora*, *P. lepidocarpodendron*, *P. neriifolia*, are among the commonest of the Macchia shrubs on mountain slopes. A few species extend eastward and northward through the tropical mountains to Abyssinia (*P. abyssinica*). Nine or ten species are recorded for Natal, several of them small trees which are dominant in the 'Protea Veld' of the Drakensberg and other mountains, growing isolated among the subtropical grasses. *P. roupelliae* is one of the commonest. *P. hirta*, a small shrub, descends to the coast.

Leucadendron has 75 species, all south-western, including the well-known *L. argenteum* (the Silver Leaf), which reaches a height of 50 feet, but according to Sim (1907) ' is native only in the neighbourhood of Capetown.' *L. plumosum* is one of the common Macchia shrubs. *Leucospermum* has 40 species in the south-west, and there is one somewhat uncertain record, *L. gerrardi*, for the Natal Drakensberg. *Leucospermum conocarpum* is often dominant in the Macchia of the Cape Peninsula.

Other genera are *Serruria* (70 species), *Spatalla* (25 species), *Sorocephalus* (12 species), *Mimetes* (20 species), *Paranomus* (15 species), *Spatallopsis* (5 species), *Aulax* (3 species), and *Brabeium stellatifolium*, all south-western. The monotypic genus *Dilobeia* occurs in Madagascar, and with *Brabeium* makes up the only African representatives of the section Persoonieae.

The Compositae are also very common in the mountain and south-western flora, but, though numerous, are, as a rule, subordinate ecologically to other Fynbosch shrubs. They more often belong to the heath stage of the plant succession in which *Elytropappus rhinocerotis* is often dominant. Associated with it are other species belonging to the same family, e.g. *Metalasia muricata, Euryops tenuissimus, Eriocephalus umbellatus.* The most important genus of the Compositae is *Helichrysum*, of which there are about 30 species in the Cape Peninsula alone, many of them common. As large or even larger is the genus *Senecio.* Both *Senecio* and *Helichrysum* are widespread over the whole of South Africa, as well as *Berkheya, Athanasia, Osteospermum, Ursinia*, etc. More characteristic of the mountains and south-west are the genera *Felicia, Corymbium, Pteronia, Mairea, Helipterum, Metalasia, Stoebe, Pterothrix, Disparago, Anaxeton, Nestlera, Relhania, Athrixia, Printzia, Othonna, Euryops.* Many of these are common not only in the south-west but also along the Drakensberg.

Some of the common species even are thus widespread, e.g. *Metalasia muricata.* The majority of the mountain and south-western Compositae are more or less woody, though often much dwarfed. Some are woody only at the base, some entirely herbaceous, and a fair number are annuals.

A number of very characteristic though small south-western families may now be grouped together. The Bruniaceae have 12 genera and 55 species. Many of them are rather common in moist places and along stream-banks, e.g. *Brunia nodiflora, Berzelia lanuginosa, Berzelia abrotanoides.* *Staavia* is another

important genus. *Berardia trigyna* is recorded for Natal. The Penaeaceae are a small family of heath-like shrubs and undershrubs, including 5 genera and 35 species (*Glischrocolla, Endonema, Penaea, Brachysiphon*, and *Sarcocolla*). The Grubbiaceae include only one genus, Grubbia, with four species. In the Myoporaceae *Oftia jasminum* is common.

In the Rutaceae the south-western section of shrubs and undershrubs (the Rutoideae) with dehiscent fruits contrasts strongly with the trees of the eastern side. The most important western genera are *Agathosma, Barosma, Diosma, Phyllosma, Adenandra, Coleonema, Acmadenia, Macrostylis*, and *Euchaetes*, including between them about 200 species, with only one, *Barosma lanceolata*, recorded for Natal. One genus, *Thamnosma* (with two species), has a curious distribution in Hereroland (South-West Protectorate) and in the island of Socotra. A detailed analysis of the whole family from the standpoint of origins and distribution would repay attention.

In the Geraniaceae the large genus *Pelargonium* (with 250 species) is a mountain and south-western type extending northwards across the tropics and producing a few species that are adapted as associated plants to grass-veld conditions, of which *P. aconitiphyllum* is abundant all through Natal. Several of the 17 recorded Natal species, however, are confined to the mountains, though nearly a dozen of them mix with the subtropical flora. The section Hoarea, consisting of stemless tuberous-rooted species, are all south-western. The section Peristera is most widely distributed, extending all over Africa, with one species in India and two in Australia. Floristically it is probably most primitive, and its habit is herbaceous like that of a Geranium. *P. grossularioides* belongs to it and extends from the Cape to the Drakensberg. The woody habit and the succulent habit seen in the Karroo species would seem to be derivative in this genus.

The Leguminosae (Papilionatae) are well represented by numerous species belonging to the genera *Cyclopia, Podalyria, Liparia, Priestleya, Amphithalea, Borbonia, Rafnia, Coelidium, Lebeckia, Viborgia, Lotononis, Aspalathus, Crotalaria, Argyrolobium, Psoralea, Indigofera, Tephrosia, Lessertia, Hallia, Virgilia, Rhynchosia*, and others. As in the case of the Compositae, some of the larger genera are distributed all over South Africa. The relatively primitive Podalyrieae are more or less confined to the mountains and south-west. *Sutherlandia frutescens, Psoralea pinnata, Tephrosia capensis, T. grandiflora, Aspalathus*

laricifolia, *A. canescens*, and *A. spinosa* are species which extend from the Cape to Natal.

The Rosaceae are, on the whole, a temperate family in South Africa, though *Rubus pinnatus*, *Pygeum africanum*, and species of *Parinarium* are subtropical. The most important mountain and south-western genus is *Cliffortia*. *C. linearifolia* is dominant in much of the Fynbosch of the Drakensberg, while *C. strobilifera* is widespread from the Cape Peninsula to Natal. One or two species of *Cliffortia* have invaded subtropical areas. *Leucosidea sericea* is an interesting monotype completely dominant in the Oudehout scrub of the Drakensberg, often forming a stage in the succession to high forest, as other Macchia shrubs (e.g. *Virgilia capensis*) do in the south-west. *Myrsine africana* (Myrsinaceae), which extends from the Cape to the Drakensberg, is another very important shrub. Like *Leucosidea*, it also forms a stage in the plant succession to scrub or forest ; in fact, it is often ousted by *Leucosidea* itself.

In the Thymelaeaceae the heath-like genus *Passerina* has several species important in the south-western Fynbosch. Other species are scattered over South Africa. Other south-western heath-like genera of the Thymelaeaceae are *Cryptadenia* (5 species), *Lachnaea* (19 species), *Struthiola* (38 species, of which 2 reach Natal). The large genus *Gnidia* is widespread. *Myrica* spp. (Myricaceae) are common in moist places and near the seashore all over South Africa. *Osyris abyssinica* (*Colpoon compressum*), the Cape Sumach, is common at the Cape and extends over the eastern side of South Africa.

In the Rhamnaceae the genus *Phylica* has a large number of south-western and mountain species.

The Selaginaceae have the genus *Selago*, with 112 species in South Africa concentrated for the most part at the Cape, but 22 reach Natal, only one or two of which descend from the mountains. Two of the South African species reach the mountains of the tropics, and there are also 17 endemic species there. *Walafrida* has 31 South African, chiefly south-western species, 1 of which extends to the tropics, 4 in tropical Africa and 1 in Madagascar. All the species of *Dischisma* (11), *Microcodon* (5), *Agathelpis* (3), and *Gosela* (1) are south-western.

Other Dicotyledonous families may be grouped together and only the most important genera will be mentioned. Ranunculaceae (*Ranunculus*, *Knowltonia*), Cruciferae (*Heliophila*, 22 species in the Cape Peninsula), Polygalaceae (*Polygala*, *Muraltia*, *Mundia spinosa*), Caryophyllaceae (*Silene*), Sterculiaceae

(*Hermannia*), Zygophyllaceae (*Zygophyllum*), Oxalidaceae (*Oxalis*, 32 species in Cape Peninsula), Crassulaceae (*Crassula, Rochea, Cotyledon*), Droseraceae (*Drosera*, 7 species in Cape Peninsula), Aizoaceae (*Mesembrianthemum, Tetragonia, Aizoon, Galenia, Pharnaceum, Adenogramma*), Umbelliferae (*Hydrocotyle, Anesorhiza, Peucedanum; P. galbanum* is very common on Table Mountain), Rubiaceae (*Oldenlandia, Anthospermum, Carpacoce, Galium*), Campanulaceae (*Lobelia, Laurentia, Cyphia, Lightfootia, Wahlenbergia, Microcodon, Roella, Prismatocarpus*), Plumbaginaceae (*Statice*, along seashore), Asclepiadaceae (various outliers), Gentianaceae (*Sebaea, Chironia, Belmontia*), Borraginaceae (*Lobostemon*), Solanaceae (*Solanum, Lycium*), Scrophulariaceae (*Diascia, Nemesia, Zalusianskya, Phyllopodium, Sutera, Manulea, Melasma, Harveya*), Lentibulariaceae (*Utricularia*), Verbenaceae (*Campylostachys, Stilbe, Bouchea*), Labiatae (*Mentha, Salvia, Stachys, Leonotis leonurus*), Polygonaceae (*Polygonum*), Loranthaceae (*Viscum*), Santalaceae (*Thesium, Thesidium*), Euphorbiaceae (*Euphorbia, Cluytia*).

The above are, for the most part, subordinate types, often herbaceous. While some of them are more or less confined to the south-west, many of them are equally common as associated plants of eastern grass-veld areas. The widespread character of subordinate genera, and especially those that appear early in the plant succession, has been already referred to more than once.

Among the Monocotyledons the most characteristic southwestern family is the Restionaceae. They are practically confined to the south-west of South Africa, Australia, New Zealand, and Tasmania, with one species in Natal (*Leptocarpus paniculatus*). The species of *Restio* formerly recorded for Natal was in error. There are also one species from Mlanje in South-East Africa (altitude 7000 feet), one species in Cochin China, and one in Chile. The South African genera (about a dozen altogether, with 230 species) grow among the Macchia shrubs on dry hillsides or are often dominant in marshes and along streams. They are very xerophytic, with leaves usually reduced to a sheath.

The most important genera are *Restio* (100 species), *Elegia* (30 species), *Hypolaena* (20 species), *Thamnochortus, Hypodiscus, Dovea* and *Leptocarpus* (15 species each). The nearly allied Centrolepidaceae are Australian with representatives in South America, while the Eriocaulaceae, which are also possibly connected, are more tropical and subtropical.

The south-western grasses have already, to a certain extent, been considered when the evolutionary history of the Gramineae was dealt with. They are, as a rule, entirely subordinate to the Macchia shrubs, though occasionally various species of *Danthonia* or *Pentaschistis* are dominant over small patches in early stages of the succession, while *Stenotaphrum glabrum* is sometimes dominant in moist places or on sandy flats.

The most important south-western genera of grasses are *Pentaschistis* (40 species), *Danthonia* (30 species), *Pentameris* (5 species), *Achneria* (9 species), *Ehrharta* (25 species), *Avenastrum* (7 species), *Lasiochloa* (3 species), *Brizopyrum* (5 species).

There are representatives also of many other genera, e.g. *Imperata arundinacea*, *Rottboellia compressa*, *Panicum* spp., *Pennisetum macrourum*, *P. thunbergii*, *Polypogon monspeliensis*, *Agrostis verticillata*, *Paspalum scrobiculatum*, *Erianthus sorghum*, *Phalaris arundinacea*, *Eragrostis* spp., etc., in dry situations. The annual grasses of the region have already been fully dealt with. The south-western Cyperaceae were also considered in Chapter VII.

FIG. 31.—*Danthonia disticha* NEES.
½ nat. size. Common. South-western and mountain grass.

In the Liliaceae the larger genera are widespread and well represented in eastern grass-veld as in the south-west, e.g. *Anthericum, Urginea, Ornithogalum, Albuca, Chlorophytum, Bulbine, Asparagus*. *Lachenalia*, however, is characteristic of the south-west.

In the Amaryllidaceae the same thing is seen. *Hypoxis, Nerine*, and *Cyrtanthus* are widespread, while most other genera are more eastern with outliers in the south-west.

In the Iridaceae, *Moraea, Aristea, Hesperantha, Watsonia*, and *Gladiolus* are all large widespread genera, but there are a number of small south-western genera: *Ferraria, Hexaglottis, Galaxia, Witsenia, Babiana, Melasphaerula, Sparaxis, Synnotia*. *Romulea* and *Bobartia* are larger and have outlying species along the Drakensberg.

The Orchidaceae are very well represented in the south-west, but again nearly all the larger genera are widespread over South Africa: *Eulophia, Holothrix, Satyrium, Disa, Corycium, Disperis*. Other genera are wholly eastern and a few are characteristically south-western. Among the latter are *Orthopenthea, Amphigena, Schizodium, Evota, Anochilus*.

The Palmiet (*Prionium*) is one of the most interesting of all, but it has already been described, and all the other smaller families of Monocotyledons belong entirely to subordinate (mostly marsh) forms and have also been included in previous chapters. The subordinate associated plants of the whole region differ from those of the tropical-subtropical areas only to a slight degree. Aquatic and marsh types are very similar all over South Africa, and many of the species, as we have seen, are widespread. The Restionaceae, however, are more or less confined to the south-west. Climbing plants, undergrowth and the associated bulbous and tuberous plants and grasses differ from those of the eastern side only in a general increase of xerophytism, and among these the genera, as a rule, if not the species, are also widespread.

The dominant shrubs of the Macchia or Fynbosch are, however, of a very distinct ecological type well expressed by the term 'sclerophyllous,' which has long been applied to it. They belong to Clements' class of Drymophytes. Their main evolutionary tendencies may be summed up briefly as follows:

1. Increased hardness of the leaves. Their leaves are full of fibre variously arranged, and though further experimental proof is desirable, there is little doubt that their resistance to water loss under conditions of extreme drought is thereby

increased. Our experiments on various Natal species in this connection have already been referred to (Bews and Aitken, 1923). The comparative rates of water loss among the south-western shrubs have, however, not yet been much investigated. It is obvious that they do show extraordinary powers of resisting water loss during the intense heat of the long dry summer.

2. Reduction in the size of the leaves. This is seen in the majority of the species. The Proteaceae, however, and other taller trees or shrubs, e.g. *Olea* spp., have retained the flat type of leaf, relying on the increased hardness only. These taller forms are dominant in climax Macchia, and since succession here as elsewhere is towards the mesophytic they may be considered more mesophytic than the lower-growing heath-like forms which appear earlier in the succession. Reduction in size of the leaves culminates in the next class.

3. The ericoid type of leaf. The leaf tends to curve downwards at the margins, enclosing the stomata on the under side. All stages of infolding may be seen. Heath-like forms are seen in a great variety of separate families. *Cliffortia* among the Rosaceae shows it, especially *C. linearifolia*, so common on the Drakensberg. The small families Penaeaceae, Geissolomataceae, Grubbiaceae, and Bruniaceae are all more or less heath-like. The Penaeaceae are allied to the Thymelaeaceae, where *Passerina*, *Struthiola*, *Lachnaea*, etc., are also mostly ericoid.

Hieronymus (in Engler and Prantl) suggests that the Grubbiaceae represents the prototype of the Santalaceae, where *Thesium* and *Thesidium*, usually hemiparasites, continue the ericoid form.

In the larger families among the Leguminosae important genera such as *Amphithalea* and *Aspalathus* (150 species) are mostly heath-like, and among the Compositae species of *Stoebe*, *Disparago*, *Metalasia*, etc., are similar. Another heath-like composite is the common, widespread, and often dominant Rhenosterbosch (*Elytropappus rhinocerotis*). The numerous Rutaceous shrubs of the south-west listed above are, to a large extent, ericoid. Among the Verbenaceae, species of *Stilbe*, *Euthystachys abbreviata*, and *Eurylobium serrulatum* are heath-like. The great culmination of the ericoid form is, of course, seen in the Ericaceae themselves, where the huge genus Erica alone has over 450 mountain and south-western species.

4. Among all the dominant shrubs there has been a general tendency towards reduction in size while retaining the woody character. Trees are very rare. With the transition to the

shrub form there is the usual increase in branching. The root systems, so far as our knowledge goes, appear to be well developed. They penetrate deeply as well as spread out widely near to the surface.

5. There is a general prevalence of minor xerophytic characters, such as hairy or woolly coverings to leaves, thick cuticle, sunk stomata, etc. Pubescence is particularly a feature of the mountain representatives, *e.g.* numerous species of *Helichrysum*, but also of some of the Proteaceae (species of *Protea*, *Leucadendron argenteum*, etc.) and some of the Leguminosae (*Podalyria*), as well as others. Such xerophytic characters, however, though common enough, are not so characteristic as the other features mentioned.

Some of the most interesting of the negative features of the Fynbosch trees and shrubs are best brought to light by comparison with xerophytic eastern types. Succulence, that common feature of the vegetation of dry regions, is not characteristic of the south-western flora. Such succulent types as do occur are largely to be considered outliers of the Karroo or eastern subtropical flora. Thorn development is also more or less characteristic only of eastern outliers in the south-west, *e.g.* species of *Gymnosporia*, *Asparagus*, *Solanum*, *Lycium*, but a few of the Macchia shrubs have prickly leaves, e.g. *Cliffortia* spp., and among the Leguminosae species of *Lebeckia*. *Viborgia*, and *Aspalathus* are often more or less spiny. *Mundia spinosa* is common. Altogether probably not more than 2 or 3 per cent. of the Macchia shrubs are spiny, a very low percentage considering the xerophytic nature of the vegetation. The compound type of leaf, which, as we have seen, is found in over 40 per cent. of eastern tree-veld and scrub species, is also rare in the south-west. A section of the genus *Cliffortia*, a few south-western genera of Leguminosae (e.g. *Cyclopia*, *Lebeckia*, *Virgilia*, *Psoralea*, *Crotalaria*), species of *Rubus*, *Peucedanum*, *Pelargonium*, and *Euryops* show it as well as outliers of eastern genera, e.g. *Rhus*, but on the whole it is not much more common than thorn development.

Though there is considerable diversity in detail among the mountain and south-western shrubs, there is, on the whole, a wonderful uniformity in the general sclerophyllous type. The distribution of this sclerophyllous vegetation is, to a large extent, determined by the seasonal rainfall. The total annual rainfall is not small—in fact, portions of the south-western region are the wettest in South Africa—but the rain falls almost entirely during the winter months, and there are several months in the

hottest summer season more or less without rain. The tallest, most mesophytic Macchia shrubs and the areas of forest occur, however, in places where the summer heat is tempered by the south-eastern mist-clouds. From these, as Marloth has shown, the deposition may be considerable, though it does not fall in such a way that it can have any effect on an ordinary rain-gauge. It drenches the vegetation, however, with moisture. On the Drakensberg the climate differs. The dry season is the winter season of low temperatures. In summer rain falls at fairly frequent intervals. Yet there are also intervals of drought in summer, and these may be rather intense. The high altitude increases evaporation during clear weather, but mist-clouds are again frequent. Though there is a marked difference in the seasonal distribution of rainfall between the eastern mountains and the south-western region, the climates of the two regions probably have more in common than at first sight might appear to be the case.

The uniformity of growth-form type in the whole temperate flora of South Africa is perhaps partly to be explained by its common origin. The dominant species belong to relatively few, though unrelated, families. At the same time, it is remarkable how widely diverse phylogenetically such a type as the heath form really is, including, as it does, a large number of the subordinate associated species.

The south-western flora of South Africa resembles closely that of the Mediterranean region ecologically. I have used the terms Macchia and Fynbosch more or less as synonymous, but the South African Fynbosch is sufficiently distinct to justify the retention of the local name. Cooper (1922) finds that the Chaparral of California is also ecologically equivalent to Macchia. His detailed analysis and descriptions of Chaparral show that it has exactly the same main characters as the South African Fynbosch. It is dominated by species belonging to genera unrelated taxonomically, the most important features of which are the root system, extensive in proportion to the size of the plant, the dense, rigid branching, and pre-eminently the leaf, which is small, thick, heavily cutinised and evergreen.

CHAPTER XI

GENERAL SUMMARY AND CONCLUSIONS

1. South Africa has many unique advantages in the study of plant distribution and the general evolutionary history of plants. It is an old land surface in direct communication with the tropics; the central portion is an elevated plateau bounded by an escarpment from which the land descends more or less steeply to the sea. Only a few of the larger rivers have cut through the escarpment, and these drain enormous areas. There are all gradations, from fertile regions of high rainfall to characteristic types of dry lands and stony or sandy deserts. The eastern, central, and north-western areas have summer rainfall, while in the extreme south-west is a region of winter rainfall and dry summers. The influence of the warmer ocean currents leads to the temperatures on the eastern side being on an average higher than on the western, so that the more tropical plants extend further south on the eastern side. Everywhere both climate and vegetation are influenced by the often highly diversified topography.

2. The flora of South Africa contains two distinct elements: (*a*) tropical-subtropical and (*b*) temperate. The tropical-subtropical element is by far the larger and occupies all the regions of summer rainfall, except to a certain extent where it mixes with the temperate element at the higher altitudes on the eastern mountain ranges. It forms many diverse types of plant community, such as mangrove forest, hygrophilous forest, mesophytic eastern high forest, mesophytic scrub, tree-veld of various kinds (Bush-veld, Brachystegia-veld, Mopane-veld, Baobab-veld, Thorn-veld with *Acacia* spp. dominant, Palm-veld, etc.), succulent and thorny scrub, grass-veld of various types, karroo and desert.

The temperate or mountain and south-western flora occupies chiefly the region of winter rainfall, but extends along the central and eastern mountain ranges of South Africa, and occurs also

on the mountains of the central tropical regions. It is of a much more homogeneous type dominated by sclerophyllous shrubs forming heath or fynbosch (macchia). In the South African flora as a whole there is to be found almost every possible variety of plant form.

3. Various systems of classifying plant growth forms or life forms have been adopted by Grisebach, Drude, Warming, Raunkiaer, Clements, and others. They have much in common, being founded chiefly on two principles enunciated by Drude, namely, (1) the rôle played by a particular species in vegetation and (2) its life history under conditions prevailing in its habitat with special reference to duration, protection, and propagation.

The arranging of plant forms in some sort of evolutionary sequence is a difficult task and would only be possible with exactitude if the past climatic history of the world were fully known. Nevertheless, a beginning has been made by Sinnott, Bailey, and others, who believe that the woody form among Angiosperms is, on the whole, more ancient than the herbaceous. The aquatic type of flowering plant is generally considered derivative as well as other subordinate types of growth form.

Botanists generally have devoted much more attention to the evolution of flower structure, yet even here there is still little agreement. Some regard simplicity in flower structure as often primitive; others, who believe in the strobiloid theory of the origin of the Angiosperms, lay stress on the idea that economy combined with efficiency has been a general guiding evolutionary principle and regard the Ranales as the most primitive Angiosperms. The Monocotyledons are now usually regarded as less primitive than the Dicotyledons.

4. There are certain types of plant habitat which existed in Cretaceous times and have remained relatively constant and uniform ever since. The most important of these are (*a*) moist tropical forest, (*b*) stream-banks and swamps, (*c*) seashore habitats, (*d*) possibly mountain habitats. It appears reasonable to suppose that primitive types of growth form are most likely to occur at the present day in such habitats.

Other types of habitat are more recent, and the growth forms of their plants are therefore in general derivative. The great grassland areas could not have existed before the evolution of the grasses, for no other group of plants could have exactly taken their place. Also dry scrub areas, semi-desert and desert areas are probably relatively recent.

While the evolution of flower structure and the evolution

of plant form have not necessarily run parallel, yet the evidence from phylogeny lends remarkable support to the view outlined. Thus, according to Engler's system of classifying the families of Angiosperms, the six most primitive orders—Verticillatae, Piperales, Salicales, Myricales, Leitneriales, Batidales—all belong to the above-mentioned primitive unchanging habitats. According to the other viewpoint the Ranales are primitive, but with very few exceptions they also belong to the same habitats. This also applies to primitive families among the Monocotyledons.

While nothing approaching a linear sequence is possible in the classification of plant forms any more than in the arrangement of families, yet any scheme of ecological classification should begin with the trees and shrubs. Of those the most primitive type appears to have been the sparingly branched hygrophilous with large undivided leaves. Within the group, reduction in size, increase of branching, reduction in the size of the leaves, increased branching of the leaf veins, the increase of fibre in the leaves, the production of compound leaves, thorn development, the development of succulence, deciduous leaves and general increase of xerophytism are some of the more important evolutionary tendencies. Associated with the trees and shrubs are various subordinate types of growth form which appear to have arisen in many different circles of affinity and are often ancient, though, as far as the Angiosperms are concerned, on the whole derivative, *e.g.* climbing plants, epiphytes, parasites, and herbaceous undergrowth or shade plants. Purely aquatic plants are considered derivative.

A new type of habitat was established after the origin of the grasses which colonised the drier land surfaces, displacing Gymnosperms. Subordinate undershrubs and increasingly xerophytic herbs were adapted to open grassland conditions.

The evidence from phylogeny is very strong in support of the view that succulence is comparatively recent. In general the angiospermous plants of semi-desert and desert conditions are all of recent form, though various xerophytic ferns and *Welwitschia* give us a hint of the types of plants that occupied such situations before the rise of the Angiosperms. Most recent of all is the annual type of flowering plant.

5. An origin for the tropical-subtropical elements of the South African flora is to be sought for in the vast reservoir of plant life in the tropics to the north. The megatherm hygrophilous forest of the tropics is probably the most ancient type

of habitat, and to a certain extent, floristically, it connects with the similar type in South America. Within the tropics there are also drier areas and, on the mountains, regions of lower temperatures which show the evolution of plant forms similar to those of South Africa. The general migration has been southwards. Purely tropical genera and species have extended farthest south along the eastern coast-belt. The numbers diminish until they are entirely replaced by allied derivative subtropical forms. In the centre and west of South Africa a very dry belt constitutes a barrier against migration southwards, so that the Karroo vegetation, the most highly evolved of all, has chiefly an eastern origin. Migration of trees and shrubs inland has taken place largely at right angles to the eastern coastline along the river-valleys and their flanks or the intervening ridges. The actual seashore is a uniform easy pathway leading to rapid migration of its own characteristic flora.

The general invasion of tropical-subtropical grasses in South Africa has also been from the north, but their lines of migration are not so easy to follow. There has been a general increase of xerophytism in the grasses as in the trees and shrubs. The numerous associated plants of grassland areas in some cases connect fairly closely with the forest or forest-margin types; in other cases, particularly the abundant geophytic Monocotyledons, their origin is more obscure. Many of the larger genera are widespread over the whole of South Africa, including the south-western region, where the dominant plants are more temperate.

The Karroo has derived its constituents partly from the eastern xerophytic scrub, partly from the xerophytic associated plants of the grass-veld and the grasses themselves, and the whole Karroo flora represents the final result of the tropical-subtropical specialisation in South Africa.

6. The temperate or mountain element of the South African flora is dominant in the south-west, but extends eastward along the Drakensberg and crosses the equator on the mountains of the tropics, reaching to Abyssinia. There are two opposing views regarding its origin, both of which may be partly correct. The one regards it as having a northern origin, the other a southern. It shows little direct connection with the tropical flora, and though possibly to be looked on as derivative, it is in many respects an old flora.

7. The evidence from phylogeny in support of the above

views is again very strong, particularly among the Dicotyledons. In over thirty families, chosen more or less at random, the tropical tribes or larger genera show relatively primitive features in the more essential flower structures, the South African representatives show relative advance. In the more superficial characters of the perianth etc., however, tropical types often show high specialisation, especially in regard to insect visits (zygomorphy, etc.). In several families the temperate south-western representatives are floristically more primitive than the derivative subtropical South African types with which they come into contact.

8. The tropical-subtropical trees and shrubs of South Africa fall naturally into three ecological classes which illustrate the principles of ecological evolution. In the first class are the Mangroves, *Barringtonia*, and various hygrophilous forest trees (e.g. *Xymalos monospora, Antidesma venosum, Bridelia micrantha, Macaranga capensis, Voacanga dregei, Conopharyngia ventricosa, Rauwolfia natalensis, Ficus* spp.).

Members of this class agree in having leaves larger than the average and nearly always simple. Thorn development and succulence are very rare or absent within the group ; however, a tendency is seen towards the development of a leathery texture in the leaves and particularly towards a decrease in size of the ' islands ' of assimilating tissue between the leaf veins.

The second class shows further advance in the evolution of form and is composed of the mesophytic forest and scrub types —a larger and more heterogeneous class. The mesophytic tall forest trees are of the most primitive form, the light-demanding forest-margin smaller trees and shrubs show evolutionary advance in form. The latter appear earlier in the plant succession. In any subtropical area, as the plant succession advances, the vegetation becomes more and more tropical. If we reverse the order of types in the plant succession we can arrange them roughly in the order of the evolution of their growth forms. The production of more xerophytic light-demanding pioneer types has enabled the more ancient hygrophilous types of Angiosperm, to extend their distribution.

In this second class of tree and shrub forms there is a higher proportion of compound leaves, a somewhat irregular deciduous tendency, the beginnings of thorn development, rather free development of coppice shoots, increased branching leading to the development of the shrub form.

The third class consists of the tree-veld and xerophytic

scrub types and is still more varied in form. It covers an enormous area in South Africa. Henkel estimates that there are 64,000 square miles in Southern Rhodesia of savannah forest (*Brachystegia*-veld, Mopane-veld, Baobab-veld, etc.). It extends through Angola on the western side. The Bush-veld of the Transvaal is similar. Thorn-veld with Acacias dominant is widespread from Natal to Damaraland. The Thorny and Succulent scrub of the eastern river-valleys represents in many respects the highest evolutionary advance and specialisation. In the still drier areas tree growth is confined to the river and stream banks. Along the coast there is a specialised sand-dune vegetation. The main evolutionary tendencies in this class are (*a*) a general decrease in size, (*b*) a marked increase in branching, (*c*) a decrease in size of the leaves, (*d*) an increase in leaf division, (*e*) a pronounced deciduous tendency, (*f*) an increase of thorn development, (*g*) an increased proportion of succulents, (*h*) a marked increase of minor xerophytic characters, particularly lignification in the assimilating organs.

9. A detailed analysis of 800 species of trees and shrubs in South Africa has been made and the percentage belonging to various types of growth form determined. Thus 15 per cent. are thorny, 31 per cent. have compound leaves, 20 per cent. have leaves over 3 inches long, 40 per cent. have leaves 3 to 1 inches long, and 9 per cent. have small leaves less than 1 inch long, and 3 per cent. are succulent. Using these percentages as a 'normal spectrum' and comparing the three classes of growth forms separately with it, the resulting statistics show very clearly the main evolutionary tendencies given above. Further statistical comparisons show that the more xerophytic tree-veld and scrub genera are more distinctly South African, being on an average as large or larger in South Africa than in the tropics, while the more hygrophilous genera are much larger in the tropics and are only represented by a few outliers in South Africa.

10. In considering various subordinate types of growth form associated with the trees and shrubs a close connection is found between forest-margin and marsh types, and many of the subordinate forms may be very ancient.

There are over 300 tropical-subtropical species of climbing plants in South Africa. Probably the most ancient form is the woody liane, which may have been derived from the much-branched slender shrub type of the forest margin. The South African forests, however, have only retained a vestige of the

rich luxuriance of the tropical forests in woody lianes. Thus *Dalbergia* has 65 species in tropical Africa and only two in South Africa, the Menispermaceae have 100 species in Africa and only 15 in South Africa, and so on. The majority of South African lianes are more xerophytic and belong to more highly advanced phylogenetic families. There are over 90 species of climbing Asclepiadaceae. The Passifloraceae and Cucurbitaceae are more often stragglers outside the forest or prostrate creepers through the grass-veld.

Epiphytes are not abundant in South Africa, either individually or as species. There are only about 45 altogether. Forest parasites are also unimportant, though there are 22 South African species of *Loranthus* and 20 of *Viscum*. Both these types of growth form are obviously derivative.

The herbaceous undergrowth of woodland is closely connected with the vegetation of the marshes, but differs chiefly in its light requirements. Some of the herbaceous shade-loving forest herbs may be very ancient. Some belong to rather primitive families such as the Piperaceae and the Araceae, but the vast majority are highly evolved, at least floristically, *e.g.* the two largest and most characteristic families, the Labiatae and Acanthaceae. Nearly all are highly adapted to insect visits.

11. The establishment of grasslands is bound up with the question of the origin of the Gramineae or of the order Glumiflorae to which they belong. There seems to be a growing consensus of opinion that the Glumiflorae are not primitive. The Gramineae, however, are more specialised and recent than the Cyperaceae; and the latter, together with many of the former, are mostly marsh types, *i.e.* they belong to one of our primitive unchanging habitats. Marsh types, however, are closely allied, as we have seen, to forest-margin types, and around the forest margins the Bamboos occur. Floristically these approach nearer than the rest of the grasses to the ordinary monocotyledonous type of flower, and they are trees or shrubs. Similarly, among the Cyperaceae there is one woody tropical genus, *Schoenodendron*, while among the Juncaceae, from which Lotsy derives the Glumiflorae, there is the woody-stemmed South African genus *Prionium*. Whether the earliest Glumiflorae were woody or not, it seems fairly certain that they were hygrophilous. But in this primitive type of habitat there are to be found herbaceous forms, some with elongated, many-noded stems, often rooting at the nodes, some with underground rhizomes and some tufted, and all responding to the demands

of increasing aridity, may have co-operated in the establishment of grasslands.

12. Among the Cyperaceae the south-western temperate South African genera *Macrochaetium* and *Tetraria* are most primitive of all, while *Schoenoxiphium*, an endemic forest-margin genus, is looked upon as the starting-point of the group of genera of which the widely distributed genus *Carex* is the most important member. The temperate genera *Schoenus*, *Lipocarpha*, *Costularia*, and *Tetraria* show connections with Australia.

The South African subtropical grasslands are dominated by members of the Andropogoneae (*Themeda*, *Andropogon*, etc.). Species of *Cymbopogon* are transitional to forest. There are many isolated vlei species belonging to such genera as *Pennisetum*, *Setaria*, *Leersia*, *Phragmites*, etc., while xerophytic forms include large numbers of species of *Aristida*, *Eragrostis*, etc. The temperate grasses belong mostly to the Aveneae, Festuceae, Phalarideae (with 6 stamens). The growth forms of South African grasses fall into the following groups arranged roughly to illustrate a possible evolutionary sequence.

(*a*) The Bamboos in a class by themselves; (*b*) Tall-growing hygrophilous, marsh and forest-margin types (*Phragmites*, *Cymbopogon*, *Erianthus*); (*c*) Hygrophilous tufted grasses (*Pennisetum*, *Setaria*); (*d*) Hygrophilous straggling or creeping grasses often rooting at the lower nodes (*Leersia*, *Panicum*); (*e*) Climbing grasses and shade-loving scrambling forest species (*Panicum*, *Olyra*, *Pollinia*, *Potamophila*); (*f*) Creeping surface-rooting and psammophilous types (*Eragrostis* spp., *Spartina*, *Cynodon*, *Stenotaphrum*); (*g*) Stoloniferous sod-forming grasses, hardly represented in South Africa except as introductions; (*h*) Mesophytic Bunch grasses (*Themeda*, *Andropogon*, *Eragrostis*); (*i*) Tussock-forming grasses (*Microchloa*, *Eragrostis*); (*k*) Xerophytic bunch grasses (*Aristida*, *Elionurus*, *Sporobolus*, *Eragrostis*) and the south-western genera *Danthonia*, *Pentaschistis*, etc., though the latter floristically are very distinct and may be rather ancient; (*l*) Annual grasses.

13. Marsh plants (Helophytes) are fairly abundant in South Africa, comprising not less than 1100 species, or between 8 and 9 per cent. of the whole flora. Among them are included some interesting types, *e.g.* Araceae (*Zantedeschia*, etc.), *Gunnera*, etc. Their growth-form characters are as follows: (*a*) nearly all are perennial herbs, but a few are slightly woody; when woody shrubs take possession the succession advances towards hygro-

philous scrub and forest; (*b*) the dominant species are nearly always Monocotyledons (grasses, sedges, Restionaceae, Typha, etc.); (*c*) underground creeping stems with adventitious roots fix the plants firmly in the shifting soil and cause dense social growth producing pure associes; (*d*) the aerial stems are usually unbranched and end in inflorescences; (*e*) many Dicotyledons are small creeping forms, others are weak stragglers; (*f*) some marsh species are xeromorphic, though all such species are apparently not necessarily true xerophytes; (*g*) the majority of marsh plants have a well-developed aeration system; (*h*) there is an absence of succulence except among halophytic species, and generally an absence of spinosity and other more pronounced xerophytic characters.

14. Water plants (Hydrophytes) are all considered derivative and show various stages of adaptation. There are some semi-aquatics which are essentially terrestrial plants that are able to live in water without marked adaptation. Amphibious forms have two or three different kinds of leaves according to where they grow. Pure aquatics may have leafy aerial shoots above the level of the water or may have only aerial inflorescences. They may be with or without the floating type of leaf, or finally may be entirely submerged with hygrophilous pollination. Very few South African aquatics belong to the Sympetalae, in sharp contrast to the undergrowth of the forest. Their main growth-form characters are well known and do not show any very interesting difference from those of the group in the world as a whole. Extreme modification is seen in the minute Algal-like forms such as *Lemna* and *Wolffia*, and also in the Podostemads and their allies (*Tristicha*, *Hydrostachys*), where the whole plant is often reduced to a thallus.

15. Seashore strand plants are nearly all fleshy and xerophytic and connect with the species of dry climatic areas. Creeping forms grow in the shifting sand nearest to the sea, upright growing species at the margins of the coast-scrub. The great majority belong to highly evolved floral types.

16. The associated plants of the grass-veld include a huge assemblage of derivative forms which gradually tend to assume dominance in the transitional area between grass-veld and karroo. Ecologically they form either vernal aspect or autumnal aspect societies, the latter more shrubby and transitional to scrub and forest, while the former are usually more or less geophytic with underground storage in rhizomes, tubers, bulbs, or in fleshy tuberous roots. Many of the genera are large

and very widespread over the whole of South Africa. Some of the genera with few or only one species are also widespread. It is very interesting to find that many genera of associated grass-veld plants are well represented in the south-western region of Fynbosch or Macchia. Many of the vernal species have a remarkable rate of assimilation in early spring, and the size of the underground storage organs is often astonishing when compared with the small aerial shoots. Nearly all of the grass-veld plants have wind-dispersal of their seeds and the majority have capsular fruits. The dry aerial shoots are all regularly burnt off once a year. Grass fires tend to favour the continuance and spread of the vernal types and to check the shrubby autumnal types.

There is much minor variation in detail of their growth forms. Rosette forms are common. Warming's classes of 'Renascent herbs with multicipital rhizomes' and 'Under-shrubs of the Labiate type' are both common and grade into one another. The 'Mat geophytes' are the bulbous and tuberous forms, and 'travelling geophytes' also occur. Creeping forms are not rare. Succulence is seen in many, but becomes more pronounced towards the Karroo. In the leaves almost every known kind of xerophytic modification is seen among the thousands of species belonging to this class.

17. The Karroo flora is the most highly specialised of all, as is shown by the dominance of recent highly evolved types such as the Compositae, especially in the transitional areas, *Mesembrianthemum* the most specialised and largest genus of the Aizoaceae, the Stapelieae section of the Asclepiadaceae, *Euphorbia* among the Euphorbiaceae, the most recent sections of the genus *Crassula*, and many other similar facts.

The growth forms of Karroo plants show the following general features: (*a*) the rocky hillsides have xerophytic trees and shrubs which connect closely with the eastern dry-valley scrub; (*b*) along the river-banks a few trees, e.g. *Acacia karroo*, *Salix capensis*, *Rhus viminalis*, *Rhus lancea*, *Zizyphus mucronata*, *Combretum erythrophyllum*, *Royena* spp., are very widely distributed; (*c*) on the plains dwarf shrubs, e.g. *Pentzia virgata*, are dominant—there is an almost total absence of green colour; (*d*) thorn development is common and often extreme; (*e*) succulence is particularly characteristic; (*f*) geophytes are common; (*g*) annuals are also common, especially in the 'opslag' vegetation which springs up after rains.

The soils of the Karroo in response to the dry climate are

generally rich in salts and sometimes excessively so. In the latter case halophytes (e.g. *Tamarix, Salsola, Atriplex*) take possession.

18. Towards the west there are stretches where extreme desert conditions prevail, especially the western litoral strip, the Namib. Under such conditions there is a vast reduction in the number of individual plants, and a reduction also in the number of species. The perennials are very xerophytic, usually either thorny or succulent or both, while there is a high proportion of short-lived annuals. While the species of the western side are often, and the genera are sometimes, endemic, while certain families, *e.g.* Amarantaceae, Scrophulariaceae, Zygophyllaceae, are unexpectedly prominent, yet, on the whole, the flora is surprisingly similar to that of the eastern side, though more xerophytic. On rocky slopes *Aloe dichotoma* and *Euphorbia* spp. are prominent, on gravel plains and sand dunes *Eragrostis spinosa, E. cyperoides, Salsola zeyheri*, and species of *Mesembrianthemum* are characteristic. *Acanthosicyos horrida* and *Sarcocaulon burmanni* are two common species.

19. The Temperate or Mountain and South-Western flora is dominated by sclerophyllous shrubs. Though it is so distinct both in origin and ecologically, it has, on the one hand, succeeded in producing genera and species which have penetrated through and even established dominance among the eastern flora, while on the other hand it has admitted many subtropical genera and species in the south-western region. Many of the elements of the south-western flora appear to be older than the subtropical eastern flora, yet the temperate flora as a whole shows complex differentiation and specialisation.

At Knysna and elsewhere there are outliers of eastern forest in the south-western region. The forest trees follow after such Fynbosch shrubs as *Virgilia capensis* in the plant succession. The Fynbosch or Macchia is, as a rule, the climax type, but an earlier stage of the succession is a low-growing type of heath with such species as *Blaeria ericoides* dominant. There is a large number of subordinate associated types, many of which, as already pointed out, are very widespread over the eastern side as well.

The Ericaceae, Proteaceae, Compositae, Rutaceae, Geraniaceae (*Pelargonium*), Leguminosae, Rosaceae, Thymelaeaceae, Rhamnaceae (*Phylica*), Selaginaceae (*Selago, Walafrida*), Bruniaceae, Penaeaceae, and Grubbiaceae are some of the most characteristic Dicotyledonous families in the temperate South

African flora, though, of course, other families are well represented. Among the Monocotyledons the Restionaceae, Gramineae (*Danthonia*, *Pentaschistis*, *Ehrharta*, *Achneria*, etc.), and numerous bulbous plants and orchids are characteristic.

The main growth-form characters and general evolutionary tendencies are as follows: (*a*) increased hardness of the leaves, (*b*) reduced size of the leaves, (*c*) the production of ericoid forms in a large number of unrelated families, (*d*) general reduction in size of the species with retention of the woody character and the production of large root systems, (*e*) a general prevalence of minor xerophytic characters such as hairy coverings to the leaves, thick cuticle, sunk stomata, etc., (*f*) comparative rarity of succulence or thorn development except among eastern outliers.

20. The whole of the argument and arrangement of the present work is based on certain ideas set forth in the second and third chapters and summarised in paragraphs 3 to 7 of this summary. If these hypotheses were based only on what we know of the geological and climatic history of the world since the rise of the Angiosperms, then they would be altogether too speculative to be worthy of serious attention. But they are supported throughout by the most generally accepted principles of the phylogenetic classification of the Angiosperms and they fit the facts of present-day distribution in both cases remarkably well. Caution, of course, is very necessary when they are applied to matters of detail. One can never be quite sure how many backward currents there have been in the onflowing evolutionary stream. At the same time there can be no doubt that geographical distribution and migration is one of the most useful keys to doubtful questions of phyletic history. It is also perfectly clear that the whole fascinating story can be read most easily in a country like South Africa, where the record has been continuous and uninterrupted for such a vast period of time.

Apart from this, the viewpoint adopted has enabled the writer—and, it is hoped, the reader also—to obtain a clearer picture of the whole vegetation of the southern half of this great continent.

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